JULIAN HIGHTOWER SINGER
Effects of Overstory Removal and Fire on Wetland Vegetation and Recruitment from the Seed Bank in a Hydrologically Restored Carolina Bay Wetland
(Under the Direction of Dr. Rebecca R. Sharitz)

Carolina bays are isolated, freshwater depressional wetlands that maintain habitat diversity along the South Atlantic Coastal Plain. The impetus for this study on Carolina bay restoration stems from the need for detailed information regarding factors influencing the restoration success of disturbed wetland ecosystems. We detail restoration treatments and subsequent herbaceous vegetation dynamics relative to changing hydrologic conditions over a two-year period post-restoration. In an initial germination project, the seed bank showed potential as an *in situ* seed source for herbaceous wetland species. Up to fifty percent of the plant species sampled two years post-restoration were present in the seed bank. More importantly, the seed bank provided wetland species in the post-restoration vegetation treatments where the canopy was removed. Two years after restoration, bay hydrology was typical of similar Carolina bay wetlands and wetland vegetation germinating from the seed bank was persisting in the wettest portions of the wetland.

INDEX WORDS: Wetland restoration, Seed bank, Carolina bay, Depression wetland

EFFECTS OF OVERSTORY REMOVAL AND FIRE ON WETLAND VEGETATION AND RECRUITMENT FROM THE SEED BANK IN A HYDROLOGICALLY RESTORED CAROLINA BAY WETLAND

by

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INTRODUCTION

In the last two decades, restoration as a practice and science has undergone substantial development. As the need for information guiding specific restoration projects has increased, the number of studies addressing the principles of restoration as a scientific endeavor has increased in step. Journals, such as *Restoration Ecology*, *Conservation Biology*, and *Ecological Applications,* have given scientists additional venues through which to present information that specifically addresses issues associated with restoration. Due to the rapid rate at which wetlands have been lost, the restoration of aquatic systems has received a large amount of interest. Efforts to restore marine ecosystems, riverine systems, and swamps such as the Everglades are well known and documented. Other freshwater, inland wetlands, such as prairie potholes of the Midwestern U.S. have been restored for waterfowl habitat. While the reasons behind restoration varies in some systems, the need for continued research on sytem-specific methods and guidelines for restoration continues to be critical to the success of restoration projects. This study focuses on the seed bank and its impact on initial wetland vegetation in light of overstory removal and burning in a Carolina bay wetland in South Carolina.

Carolina bay wetlands are freshwater, isolated, depressional wetlands located on the Atlantic Coastal Plain. These wetlands are typically not thought to have a significant connection to regional groundwater, but are instead, influenced by precipitation patterns that can vary with cyclical climate changes. Lide et al. (1995) did find that the hydrology in one bay was influenced by groundwater when the bay was filled to maximum water levels for prolonged periods of time. The number of Carolina bays on the landscape has been debated. Prouty (1952) estimated that there were up to 500,000 bays located across their range from Georgia to Maryland, with the highest concentration located along the lower Coastal Plain of South Carolina and North Carolina. Later studies have estimated the numbers of Carolina bays as 20,000 (Richardson and Gibbons 1993; Sharitz and Gresham 1998). The discrepancy may be explained by the lack of formal definition of Carolina bays and similar depression wetlands occurring within the range. Most definitions of Carolina bays focus on their geomorphic features, which consist of an elliptical shape oriented Northwest to Southeast along the long axis and a sand rim. Lide (1997) suggests that the degree to which many of these wetlands has been influenced by anthropogenic activities may be one factor that has led to the disparity in estimated numbers.

In fact, Bennet and Nelson (1991) estimated that 97 percent of the bays in South Carolina have been disturbed to some degree. The primary disturbance in bays is usually simple hydrologic alteration for agricultural purposes. The degree to which these wetlands are altered may have a direct bearing on how easily they can be restored. If the hydrology of the wetland can be restored and wetland plant species established, the function of the wetland as a habitat for species of flora and fauna may be enhanced in a relatively simple manner.

Typical bay hydrology can vary on a climatic cycle. In many bays, long periods of drier than average conditions are commonly associated with complete hydrologic drawdown. During these times of drought, fire may easily spread through portions of the bay from the surrounding upland (Kirkman 1992). The lack of peat found in bays on the upper Coastal Plain is thought to be evidence of periodic drawdown and oxidizing events (Schalles and Shure 1989). Charcoal evidence found in several studies (Buell 1946; Schalles 1979) suggests that bays burn periodically. Fire may play an important role in maintaining communities within Carolina bays. Kirkman (1995) suggests that fire during periods of drought can promote species richness in depressional meadows dominated by sedges and grasses. Fires occurring in winter followed by flooding can lead to changes in dominance of vegetation within the depression (Kirkman 1995).

Also associated with Carolina bays' varied hydrology are cyclical changes in extant vegetation (Kirkman 1992; Kirkman and Sharitz 1994). In some ways, bay vegetation dynamics may be similar to those in similar depression wetlands elsewhere in the U.S. Van der Valk (1981) proposed a model for prairie pothole wetlands in which changes in floristic composition could be predicted from the life-history characteristics of species in the seed bank. Van der Valk (1981) concluded that hydrology acted as a filter, through which certain species could exist in the extant vegetation as conditions for species-specific germination were met. Thus, suites of species would be associated with changing hydrology, varying with climatic patterns over time. Collins and Battaglia (2001) assert that hydrology did act as a filter for recruitment from the propagule bank and for species distribution across the depth gradient for six bays in South Carolina.

From a restoration perspective, the presence of an intact seed bank that includes wetland species may be paramount to vegetation recovery in a system where hydrology has been restored. Restoration in other freshwater systems has focused on intensive planting and/or donor soils in efforts to quickly establish wetland vegetation (Vivian-

Smith and Handel 1996; Brown and Bedford 1997). The specific objectives of this study were:

Vegetation Component:

1. To determine if the hydrology of a drained Carolina bay could be restored.

2. To compare the effectiveness of different site treatments in promoting wetland vegetation re-establishment.

3. To examine wetland plant species recruitment across the restored hydrologic gradient.

4. To determine the success of wetland vegetation reestablishment.

Seed bank Component:

1. To analyze the content of the remnant seed bank after more than forty years of altered hydrology in order to determine if wetland species were present.

2. To determine if restoration treatments imposed on the bay affected the germination of wetland species in the seed bank.

3. To examine the spatial distribution of seed bank species germinating into the bay across the depth and hydrologic gradient.

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CHAPTER 1:
THE EFFECTS OF OVERSTORY REMOVAL AND BURNING ON THE INITIAL HERBACEOUS VEGETATION DEVELOPMENT IN A CAROLINA BAY WETLAND[1]

[1]Singer, J.S. and R.R. Sharitz to be submitted to *Restoration Ecology*

Introduction

As human impacts on nature have increased dramatically within the past several generations, more focus has been directed toward restoration of impacted natural systems. The inherent loss of diversity and environmental quality associated with the loss of critical habitats have driven elements of public opinion toward actions attempting to limit future losses and to restore habitats degraded by anthropogenic activity. The scientific community has progressed in efforts to provide knowledge and direction to those restorative actions over the last twenty-five years. The success of scientific journals publishing articles on restoration, such as *Restoration Ecology*, *Ecological Applications*, and *Conservation Ecology*, are testament to the fact that new ideas and examples of restoration in natural science are progressing with rapidity. Even so, practical restoration can be a difficult undertaking. Restoration projects often involve private, public, and government interests that are not completely compatible at all times. An area that has received particular interest from both the public and scientific community is wetland restoration.

Wetland loss over the past two hundred years has been dramatic in most of the United States. An estimated 392 million acres of wetlands existed in the area of the fifty states as of the late eighteenth century. In the lower forty-eight states, roughly fifty-three percent of the wetlands that existed in the late 1700's have been lost (Dahl 2000). By the 1980's the area of the coterminous U.S. that could be characterized as wetland had decreased from eleven percent to five percent (NAS 1992). An important factor in wetland loss has been agricultural development. According to a report by the National

Resource Council (NRC), eighty percent of the historic freshwater wetlands have been lost due to agricultural conversion (NAS 1992)

Restoration, as defined by the NRC, is returning an ecosystem to a close approximation of its condition prior to disturbance. Accomplishing restoration means ensuring that ecosystem structure and function are recreated or repaired and that natural dynamic ecosystem processes are operating effectively again (NAS 1992). In the face of wetland loss and degradation the means by which structure and function are restored has become the focus of much research.

A concerted effort has been made to restore wetlands in recent years. The impetus for this restoration surge has come from multiple sources. As the overall number of wetlands decreases, the importance of remaining wetlands as habitat and for water quality protection increases. Public awareness of wetland values has grown and the positive ecological implications inherent in wetland restoration have become more obvious. Federal agencies such as the U.S. Army Corps of Engineers and the Environmental Protection Agency that provide support for mitigation banking, and programs such as the Natural Resources Conservation Service's Wetlands Reserve Program, have made restoration more compatible with industrial development and agricultural practices.

In spite of the increased interest in wetland restoration, however, the ecological methods behind restoration implementation are still poorly understood. The amount of effort spent on the restoration varies widely from intensive site preparation and replanting to relatively simple hydrologic adjustments. Establishing goals for each restoration based on sound ecological principles should help define the degree to which restoration efforts are implemented. Allowing post-restoration conditions to follow a "self-designing restoration" (Mitsch and Wilson 1996), or a pattern of natural successional development, may require less human intervention toward those established restoration goals. Restorations following the self-design approach may require a better understanding of site-specific characteristics such as sources of wetland vegetation and knowledge about hydrologic inputs (Galatowitsch and van der Valk 1996a).

The degree to which restoration of degraded wetlands has been studied varies with type of wetland and region. Coastal restoration projects have been researched much more intensely than freshwater, inland wetlands (Zedler 1993; Zedler and Callaway 1999). Many of the numerous wetland restorations attempted in freshwater systems involve short-term monitoring, but a few have implemented long-term monitoring in order to formally document restoration success (Reinartz and Warne 1993). These studies again emphasize the need for clear restoration goals and established monitoring plans over time.

In efforts to fill the knowledge gap with respect to freshwater wetland restoration, there are a growing number of studies directed toward quantifying the parameters associated with wetland functions. These studies may aid in establishing clearer goals for restoration and wetland monitoring. Bishel-Machung et al. (1996) examined 44 created wetlands and 20 reference wetlands in Pennsylvania and found significantly differing wetland soil properties between the two groups. They suggested that the soil differences were the primary reason the created wetlands did not compare favorably with reference sites in other more commonly examined wetland parameters such as vegetation and water chemistry. Wilson and Mitsch (1996) focused on assessing the legal success as well as functional success of five wetlands of varying ages created for mitigation purposes in Ohio by measuring hydrology, soils, vegetation, wildlife, and water quality. They concluded that legal permitting for mitigation was decoupled from the logical natural guidelines used to assess function in the field. Legal requirements stipulated at the beginning of the mitigation project focused on the amount of area restored rather than the functional parameters measured, and led to discrepancies in the quality of wetlands when compared to reference wetlands in some cases.

Certain freshwater wetland types of the United States have received more attention than others. The prairie pothole or kettle wetlands of Iowa, Wisconsin, and Minnesota have been studied more intensively than many freshwater wetlands, partly because of their importance as waterfowl habitat. Restoration efforts in these isolated, depression wetlands focus on natural colonization of native species and restoring the hydrology rather than intensive plantings as is often done in restoration of other types of systems (Galatowitsch and van der Valk 1996a). Vegetation establishment in the years following restoration is limited by slow dispersal of some plant guilds found in natural prairie pothole wetlands (Galatowitsch and van der Valk 1996b). Also, Reinartz and Warne (1993) found that age and proximity to other wetlands increased the diversity of native wetland plants in created, isolated, depression wetlands in Wisconsin.

Carolina bays are similar to prairie potholes in that they are depression wetlands isolated on the landscape. Bays are distributed throughout the South Atlantic Coastal Plain of the U.S. from Georgia into New Jersey, with the highest concentration occurring in North Carolina and South Carolina (Johnson 1942; Prouty 1952). Carolina bays are elliptical, shallow wetlands ranging in size from less than fifty meters to over eight kilometers in length (Richardson and Gibbons 1993; Sharitz and Gresham 1998).

The hydrology of Carolina bays is varied. Bays may be continuously flooded, seasonally flooded, or rarely flooded. There are typically no surface inflows or outflows, making the hydrologic regime dependent upon precipitation for recharge (Schalles and Shure 1989). An impervious clay lens typically restricts influences from groundwater. However, in a study of one bay, Lide et al. (1995) demonstrated that interactions with the water table could occur even though the hydrologic regime was predominantly dependent upon precipitation and evapotranspiration. Variability of hydroperiods between bays is common even though they may be in close proximity and receive similar amounts of precipitation (Sharitz and Gresham 1998).

The vegetation found in Carolina bays is greatly influenced by hydrology and substrate, and often exhibits a pattern of species zonation along the water depth gradient from the center to the outside rim of the bay (Sharitz and Gibbons 1982). Bennett and Nelson (1991) described eleven vegetation types associated with Carolina bays in South Carolina, ranging from oak hickory scrub on the outside rim to depression meadow in the interior. The development of these vegetation types was intimately linked with bay disturbance history and hydrology. De Steven and Toner (1997) and De Steven (1994) also described vegetation development in Carolina bays on the upper Coastal Plain of South Carolina. These authors determined that a bay's projected vegetation type was linked to hydrology and also to the depth to the clay lens and the geomorphology of the basin. Shallow clay lenses tended to support more variable hydroperiods and these bays were usually dominated by woody species. The dependency on hydrology suggests that vegetation of Carolina bay wetlands should be dynamic and undergo changes as precipitation, and water levels, vary. Since the hydrology of bays is dependent primarily upon precipitation, the vegetation should undergo shifts as precipitation varies with climatic changes. Kirkman (1992) described the vegetation shifting dynamically from floating aquatics to meadow grass species to pines as depth and length of flooding change with cycles of drought and precipitation.

Carolina bays may have potential as wetland restoration sites. There are a large number of bays on a landscape that has a history of intensive agricultural use, and the farmers attempting to increase arable land drained many bays with simple ditches. By plugging these ditches, it may be relatively easy to restore the natural hydrology of drained bays. Also, even though bays are isolated from other wetlands on the landscape, the viability of an intact seed bank is an unexplored source of species for natural re-colonization of restored bays.

Whether or not a wetland can attain an acceptable level of restoration success may be dependent on how disturbed the wetland has been (NAS 1992). For example, the ability of drained prairie pothole wetlands to naturally regenerate vegetation similar to undisturbed wetlands has been questioned recently (Galatowitsch and van der Valk, 1996a; Galatowitsch and van der Valk 1996b; Mitsch and Wilson 1996). While a number of Carolina bays have been permanently destroyed by industrial and commercial development, the majority of bays have been disturbed less severely through agricultural conversion and logging (Bennett and Nelson 1991).

The goals of Carolina bay restoration may be less complex than goals of restoring other wetlands. Because bays are depressions, their primary values are in habitat as opposed to values associated with water quality and flood control. Thus, the primary goal for bay restoration becomes the development of conditions that support the establishment and maintenance of wetland biota. This study assessed the feasibility of Carolina bay restoration using simple and cost effective treatments that promote natural regeneration of wetland plant species. Specific goals were:

1. To determine if the original hydrology of a drained Carolina bay could be restored.
2. To compare the effectiveness of different site treatments in promoting wetland vegetation re-establishment.
3. To examine wetland plant species recruitment across the restored hydrologic gradient.
4. To determine the success of wetland vegetation re-establishment.

Methods

Study Site

In the spring of 1993 a small (4.25 ha), drained Carolina bay (Bay 93) on the Department of Energy (DOE) Savannah River Site (SRS) in Barnwell County, South Carolina was chosen for habitat restoration. DOE expressed further interest in exploring the potential of Carolina bay wetland restoration for mitigation banking purposes. Aerial photography from 1949 and 1951 suggested that the bay supported herbaceous wetland vegetation at that time. It is apparent from these photographs that the bay was ditched before 1951. In the years following this hydrologic disturbance, the drained bay became dominated by non-wetland vegetation. At the time the study was initiated, the vegetation was predominantly *Pinus taeda* and *Liquidambar styraciflua,* as well as *Rubus* spp. and *Smilax* spp. There was very little herbaceous vegetation in the understory, however, a few wetland species remained in the deepest portion of the bay.

Topography

In the summer of 1993 a general topographic survey was completed in order to assess the dimensions and contours of Bay 93. Elevation measurements were recorded at 5 m intervals along transects radiating outward from the center of the bay using a laser level. A topographic map was generated from these data using a mapping program with a krieging function (Golden Software 1999). It was determined from the topographic map that the deepest point in the bay was offset from the geographic center of the bay. The bay was divided into four wedges, each beginning at the deepest point of the bay and extending outward to the bay rim (Figure 1).

Hydrology

The drainage ditch was closed with an earthen dam in September of 1993. Interpretation of the hydrologic data concentrated on describing the effects of plugging the drainage ditch. Pre-restoration hydrologic conditions were not available, but the water budget was evaluated using the Thornthwaite method (Thornthwaite and Mather, 1955). Bay volume and area calculations were based on Surfer 7.0 (Golden Software 1999) contour output and the integrated volume below the bay rim. Water levels in the bay were estimated with a simple hydrologic model using monthly rainfall as the primary water source, and potential evapotranspiration (PET) following Thornthwaite and Mather (1955) and water loss through the ditch as the primary losses. The volume of water lost through the ditch was estimated using Manning's equation (Dunne and Leopold 1978). Post-treatment hydrologic data were recorded with a Steven's water level gauge, digitized, and plotted. These data were compared to the vegetation plot elevations (see below) to examine the degree (water depth and duration of flooding) to which each plot was inundated during the growing season. Precipitation and temperature data were gathered from the National Oceanic and Atmospheric Administration's Blackville 3W permanent weather station located approximately 18 miles from Carolina bay 93 in Blackville, SC.

Vegetation

A transect extending across the elevation gradient was randomly established in each of the four sections for vegetation sampling. Ten sample points were established along each transect according to elevation (every decimeter of increase). At each sample point along each transect, five 1 m^2 herbaceous sampling plots were placed along a line perpendicular to the transect. At alternate sample points along the transect, one 20 m by 5 m tree plot was established and two 2.5 m by 5 m shrub plots were placed within it (Figure 2).

In August 1993 pre-restoration base line vegetation data were collected. In the 1 m^2 plots herbs, small vines, and woody seedlings (< 1.4 m tall) were tallied by species and percent cover was estimated on a scale of 1 to 5 (noting r for trace or rare amounts with insignificant cover) according to the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974). Stems were counted for all individuals unless seedling density of a species made individuals too difficult to discern. In this case individuals were counted for a smaller area and the total numbers in the plot were estimated. In the shrub plots all shrubs, saplings and larger vines (> 1.4 m and < 4 cm diameter at breast height, DBH) were tallied by species. Finally, in the 20 m by 5 m plots trees (> 4 cm DBH) were tallied by species. The 1 m^2 plots were re-sampled in the two growing seasons following restoration treatments (1994 and 1995).

Nomenclature follows that of Godfrey and Wooten (1979). Individuals not included in Godfrey and Wooten were identified using Radford et al. (1968). Questionable identifications were referenced with herbarium specimens at the Savannah River Ecology Laboratory in an effort to limit misidentification. The following analyses focus on the species level of detail unless otherwise stated.

For the purpose of restoration, several treatments were chosen to facilitate wetland vegetation re-establishment. These treatments included restoration of the bay's water holding capacity by closing the drainage ditch, removal of non-wetland woody vegetation (clear-cutting), and burning of the litter layer. The burned / cut and cut sections of the bay were clear-cut prior to the closure of the ditch and the burned / cut and burned sections of the bay were burned in January of 1994. One section of the bay remained intact as a control (Figure 1). The design thus provided no replication of treatment across bays or within the bay, which limits the interpretation of the findings and extrapolation to other bay restorations.

Analysis

All statistical evaluations were performed with SAS 8.0 (SAS 2000). Proc GLM was used for analysis of variance and significance testing of species richness and wetland site scores to account for missing or zero values present in certain portions of the data set. The differences between treatments, as well as the differences by position along the elevation gradient within each treatment were examined. Interactions between position and treatment were included as explanatory elements of the statistical model.

Species richness and wetland site score statistics were calculated on count data at the plot level. For both the between treatment effects and within treatment effects, a wetland score was calculated for each 1 m^2 plot using the weighted average of national wetland indicator status (NWI) values for the Southeast (Reed 1988). The NWI describes the probability distribution of finding a given species in a wetland habitat. The values range from 1 to 5 with corresponding designations of obligate wetland, facultative wetland, facultative, facultative upland, and obligate upland. An obligate wetland species has a .99 probability of occurrence in a habitat that will be a jurisdictional wetland. The following designations, facultative wetland through obligate upland, indicate probabilities of .67, .50, .33, and .01, respectively, of occurring in a wetland. The formula used for calculating the wetland site scores for each elevation along the transect summed the number of stems for each species in each 1 m^2 plot and multiplied by each species' wetland indicator status. These site scores were evaluated with the following equation:

$$\text{Wetland Site Score} = (\Sigma Aij * NWI)/ \Sigma Aij$$

where A was defined as the number of species, i was the 1 m^2 plot, and j was the sample point (elevation position) along the sample transect. The wetland scores for each 1 m^2 plot were averaged by elevation position and the means and standard errors were calculated. The resulting wetland score corresponds to a position along the elevation gradient from the center to the edge of the bay. Proc GLM was used to test for differences between least square means of wetland site scores for treatment and position effects. The numbers of individuals found in the sample plots were used as weights for the analysis of treatment and position effects on site scores.

Results

Topography

Elevation data taken within Bay 93 showed a relative depth range from 0.0 m in the deepest natural area of the bay to 1.10 m at the outside rim. Because the deepest area in the bay was offset from the geographic center, the slope from the center to the rim varied throughout the bay (Figure 3). The ditch draining the bay in the southwest quadrant extended from the deepest area through the outside rim. The ditch was 0.45 m below the natural lowest area in the bay. Disregarding the volume of the ditch, the total volume of the bay calculated from the elevation at the top of the weir was 14000 m^3. The total volume of the ditch was 55 m^3, approximately 250 times less than that of the bay.

Hydrologic restoration

Water level recordings taken in the bay show that the hydrology was restored over the three-year sampling period (Figure 4). Prior to restoration the bay held water from time to time, at least briefly, and water was occasionally observed to be pouring out of the ditch. The bay was dry for much of the year prior to pre-restoration sampling. The hydrograph shows that ponding occurred in the bay in the first winter after the closing of the ditch. At 0.45 m or greater, water levels exceeded the capacity of the ditch and flooding began in the lowest areas of the bay. In the summer following the initial restoration efforts (1994), the bay did dry down completely. In the second winter after restoration treatments, the water levels rose again and a portion of the bay remained ponded throughout the second growing season.

Precipitation during the winter of 1994 and 1995 was roughly equivalent although monthly variations were apparent (Figure 5). This pattern suggests that the sediments within the bay may have needed time to become saturated enough to hold water at the ponded stage for extended periods of time. The combination of saturated soils and more precipitation in the second growing season after restoration resulted in continuous ponding in the bay. During the first winter after the ditch was closed, pond stage reached .76 m above the bottom of the ditch. This water level inundated position 4 in each of the treatment areas. In the second winter and early spring, water levels increased to 1.2 m above the bottom of the ditch and inundated position 8 in each treatment (Figure 4). Positions 1 and 2 in the center of the bay remained inundated throughout the remainder of 1995. Position 3 remained flooded all but 15 days of the 1995 growing season. Positions 4 and 5 were subjected to the largest number of wetting and drying events and these positions could be classified as transitional between standing water and dry conditions.

Positions 6 through 8 were flooded for relatively short periods of time, each higher elevation drying out earlier in the 1995 growing season. Positions 9 and 10, near the rim of the bay, were not flooded at any time during 1994 or 1995.

Evidence from the water budget calculations show that hydrology of the bay before the ditch was plugged was substantially different from that after the ditch was closed in 1993. The precipitation and potential evapotranspiration patterns for the years after the restoration do not differ from the years prior to the restoration (Figure 6). Precipitation and evapotranspiration constituted the principal components of the water budget for the bay after the ditch was closed. The ditch leading out of the bay was an effective drain, and prior to its closure the water loss through the ditch substantially impacted the maximum water levels within the bay as well as the duration of flooding. A conservative estimate of the ditch effects was calculated with water flowing at the lowest hydraulic gradient that corresponded to filling of the ditch to .1 m. The flow rate exiting the bay through the ditch under these conditions was estimated to be approximately 27,000 m^3 / month. At this flow rate the entire volume of the bay (14000 m^3) would be drained in 15 days. Even though these numbers assume the ditch was perfectly efficient in draining the bay, which it may not have been, it is obvious that the ditch dominated the water budget of the bay prior to restoration treatment. Water losses from the bay were nominal after restoration. The greatest losses were due primarily to evapotranspiration during the growing season (Figure 6). There were short periods of time in late spring of each year when potential evapotranspiration (PET) losses exceeded precipitation inputs. With the exception of these short periods, the bay was not in a moisture deficit for the majority of the growing season after the effects of the ditch were removed.

Vegetation

Total species richness prior to restoration was very low in all treatment areas. Only twelve herbaceous species were found in the bay (Table 1), and there was a maximum of four herbaceous species in any of the 1 m^2 plots. Only two species, *Carex crinita* and *Carex glauscecens* occurred in all four treatment areas. These two species were located in the deeper area of the bay, thus even though they were in all treatment areas their percent cover over the entire bay remained low. Several species were locally abundant: *Andropogon virginicus*, *Asplenium platyneuron*, *Galium filifolium*, *Galium obtusum*, and *Hypericum hypericoides*. However, percent cover in the herb layer for all species was low. Total richness increased greatly in the two years following restoration treatments (Table 1). The increase was most apparent in the clear-cut portions of the bay rather than in the control or burned treatment areas. The number of taxa sampled in both the control and burned treatments in 1994 and 1995 remained as low as in the pre-treatment sampling. The total number of species sampled across the entire bay increased to more than fifty.

Mean species richness per m^2 increased dramatically following restoration in both cut and burned / cut treatment areas (Figure 7). These two treatments were not significantly different from each other in 1994 and both differed from the control and burned areas in 1994 and 1995 (Table 2). Burning alone had little effect and species richness in burned areas was not different from that of the controls (Table 2). Position effects were also significant in 1993 and 1995 for species richness (Table 3). *Andropogon virginicus* and *Hypericum hypericoides* were present in all sites for both post-treatment years. In 1995 *Leersia hexandra* was also found in all four treatments. Several species such as *Echinodorus parvulus*, *Carex walteriana*, and *Panicum* *sphaerocarpon*, which were not present in 1993, became predominant in the cut and burned / cut treatment areas by 1995 (Table 4), and *Carex walteriana*, *Leersia hexandra,* and *Juncus repens* formed large patches in these two cut areas. There was an increase in some upland weedy species such as *Erichtites hieracifolia* and *Eupatorium* spp. in the first year following treatments. These species tended to decline, *Erichtites hieracifolia* most dramatically, at lower elevations under the more inundated conditions of 1995 (Table 4). Some wetland species such as *Utricularia biflora* and *Utricularia inflata* were found in great number in the more inundated conditions of 1995.

Patterns of species richness were not readily apparent across the elevation gradient in 1994 (Table 5); however, by 1995 there was a clear pattern of higher species richness per m^2 in higher portions of the bay and lower species richness per m^2 at lower elevations. In 1994 there was a mix of wetland and non-wetland species along the elevation gradients in the cut and burned / cut treatment areas (Figure 8). By 1995, the plots in the lower half of the gradient contained predominantly obligate or facultative wetland species (Figure 9), and in some plots only obligate species were found. The one upland species found in the second to lowest portion of the bay in 1995 was located on a stump mound above the water level. The lowest species richness occurred in plots at positions 3 and 4 of the cut treatment where large dense patches of *Echinodorus parvulus* and *Carex walteriana* were dominant. The shifting of species along the hydrologic gradient resulted in zones of vegetation forming along the sample transects from the bay center to its outside edge. Submerged or floating aquatics flourished in the deepest portions of the bay. By 1995 *Panicum* and *Rhexia* spp. were established in an intermediate zone in which the highest water fluctuations occurred. Upland species remained in the plots at positions 6 through 10 above the water levels reached during the growing season in both 1994 and 1995.

The wetland site scores were utilized to evaluate changes in vegetation types in response to changing hydrologic conditions over time. As water levels fluctuate, the distribution of species along the elevation gradient should be correlated with the wetland site score, which is an indicator of wetland character. A lower wetland score would indicate more dominance by wetland species for a particular position along the sample transect.

Initial wetland site scores within the bay were influenced by the low species richness and small number of individuals found in any plot. In contrast to species richness, subsequent comparisons of site scores following the restoration treatments demonstrated little treatment effect (Table 6, 7). The cut and burned / cut treatments were not significantly lower than the control and burned treatments in 1994 or 1995. Also, the control and burned treatment areas were not significantly different from one another. Clear-cutting the bay had the most significant impact on species richness and composition, but not necessarily on wetland sites score values. It is important to note that missing values due to lack of plants sampled in the plots occurred throughout the bay in 1993 and in the control and burned treatment areas in 1994 and 1995 (Table 6). For site score analysis, these values were treated as missing in order to limit the effects of having scores of zero that would artificially lower the average. The mean wetland site score values for all treatments did decrease from 1993 to 1995, indicating that more wetland species were present in all treatments (Table 7).

When the site scores were evaluated with respect to position along the elevation gradient, trends in wetland vegetation establishment became more apparent. In 1994, the site scores for the highest two positions along the gradient were drier than those for the lowest two positions. However, there was no clear pattern of site scores for the positions in the middle of the elevation gradient (Table 7). The 1995 data show the site scores increasing along the elevation gradient from low values in positions 1 through 5 and higher values in positions 6 through 10.

In order to focus more intently on the effects of elevational position on wetland vegetation, further analysis was carried out on the cut and burned / cut treatments areas. These clear-cut treatments were not significantly different and had no missing values along the elevation gradient in the post-restoration treatments (Table 6). In 1994, although least square means of wetland site scores were generally ordered from lowest to highest position, there was no noticeable statistically significant difference in the means across the elevation gradient (Table 8). By 1995, however, the least square means for positions 1 through 5 were more similar to each other, as were the means for positions 8 through 10.

Interaction between treatment and position was significant in 1994 ($p = .0441$, Table 3); however, this interaction effect is not present in 1995. The increase in the F statistic for position effects by 1995 suggests that elevation and hydrologic factors are beginning to sort out species along those corresponding gradients. A linear regression analysis performed on position and wetland site score in both 1994 and 1995 revealed the developing linear relationship between site score and position along the elevation gradient. The increasing positive relationship of site score with position between years was evident for all treatments (1994, $F = 51.25$. $p = .0001$, $r^2 = .243$; 1995, $F = 152.56$, $p = .0001$, $r^2 = .538$, Figure 10). The relationship between wetland site score and position along the elevation gradient is even stronger for the clear-cut portions of the bay (1994, $F = 61.00$, $p = .0001$, $r^2 = .376$; 1995, $F = 288.16$, $p = .0001$, $r^2 = .740$, Figure 11).

The differences in site scores from 1994 to 1995 demonstrate the degree of wetland vegetation change within the bay. At all positions but 7, the site scores for all treatments decreased from 1994 to 1995 (Table 9). Position 7 also had the highest standard error term of all positions, indicating plot variability at that elevation. The plots at positions 3 through 5 that were not flooded during the first growing season, but were inundated for portions of the second growing season, show the largest drop in wetland site scores. These transitional plots at position 3 through 5 correspond to the areas where *Panicum* spp., *Rhexia mariana*, and *Rhexia virginica* were establishing zonal patterns typically found in Carolina bays. The effect of increased water levels during the growing season on species change in 1995 is even more apparent for the two clear-cut treatment areas (Table 10).

Discussion

<u>Hydrology</u>

The success of restoration in Carolina Bay 93 can be evaluated through functional hydrologic changes as well as vegetation characteristics. Ponding occurred in the central portion of the bay in the first winter after the closing of the drainage ditch. In the subsequent year, the hydrologic pattern observed in the bay continued to conform to hydrologic patterns consistent with other natural bays in the region (Lide et al. 1995; Sharitz and Gresham 1998). A typical water pattern includes higher water level in late winter and spring resulting from higher rainfall and lower evapotranspiration. This is followed by lower water levels in the summer and fall months as evapotranspiration increases and precipitation decreases. This typical Carolina bay hydroperiod did not occur before restoration, but was established in Bay 93 within two years following closure of the ditch. The importance of the ditch and how much it influenced the hydrology of the bay cannot be overstated. The potential volume of water exiting the bay far outweighed the rainfall and evapotranspiration elements of the water budget. Rainfall is only slightly greater than PET in many depression wetlands that are seemingly isolated from regional groundwater sources. The volume of water lost through the ditch substantially altered that balance towards much drier conditions. In Bay 93 the ditch was particularly effective because it intersected and drained the lowest portion of the bay. In other depression wetlands similarly ditched, the effect may also be dependent on geomorphology.

Vegetation

The removal of the dominant overstory vegetation had the most dramatic effect on herbaceous vegetation re-establishment in Bay 93. Tree removal increased light levels within the bay and could have provided an opportunity for germination of species from the seed bank and other seed sources. This is most evident in the species richness and site score values for both clear-cut treatment areas both years after restoration. Soil disturbances associated with the logging process also were likely to have contributed to seed germination and vegetation establishment. This disturbance provided mineral soil for germination of seeds dispersed into the bay and could have brought buried seeds present in the seed bank to the surface where they could germinate. Similarly, Kirkman (1992) found significant increases in species richness for tilled plots in four depression meadow Carolina bays dominated by graminoid species. The areas of Bay 93 that were not clear-cut remained low in species richness even if they were burned. This suggests that removal of the surface litter and exposure of mineral soil alone may not have been adequate to establish herbaceous vegetation. In support of this, Kirkman (1995) found that burning, an effective method for removing litter that mimics natural processes, increased species richness in only one of six herbaceous vegetation types. However, in three lacustrine wetlands in Canada, there were marked increases in seed germination when litter was removed from experimental field plots (van der Valk 1986). The effectiveness of the litter removal through burning in Bay 93 is questionable. The burning occurred after the clear-cutting treatment was implemented. In the burned treatment area litter was removed down to mineral soil, but in the burned / cut treatment area burning was patchy due to bare soil and debris piles resulting from the logging.

The conditions present after overstory removal allowed establishment of a large number of wetland and non-wetland species from a variety of seed sources. The initial influx of diverse species began to sort out along the elevational gradient as the hydrologic gradient became reestablished after the ditch was closed. By the second growing season after restoration treatments were imposed, wetland and non-wetland plants were beginning to form distinctive zones across the hydrologic and depth gradient.

Other environmental conditions may also vary along this gradient and could affect germination and establishment of wetland species. Soil chemistry and physical properties were found to change from the center of Bay 93 to the outside rim. Reese and Moorhead (1996) found that clay content, organic carbon, and CEC were higher in the center of the bay and decreased significantly toward the rim. Sand content was high (70-78%) and increased at the rim of the bay; silt content ranged from 15-21 % with no pattern of change across the gradient. In addition, pH was low in the bay interior and increased toward the rim (4.6-5.3). Exchangeable cations (Ca, Mg, and K) were low throughout the bay and did not show significant changes along the gradient. Studies in other Carolina bays have demonstrated that N and P did show a weak gradient associated with depth (Miller 2000). In established bays, low nutrient concentrations may be limiting to plants across the entire elevation gradient (Miller 2000). However, it is not apparent if this is true for recently inundated bays such as Bay 93 that have undergone fundamental hydrologic changes over time. These soil factors, particularly clay content, organic carbon and CEC, could have influenced plant growth responses after germination and contributed to the zonation patterns that developed.

The vegetation patterns seen in Bay 93 after restoration treatments were typical of those reported in other herbaceous meadow Carolina bays within the region (Kelley and Batson 1955; Schalles and Shure 1989; Kirkman 1992). In particular, the center of the bay was dominated by the submersed species *Utricularia biflora* and *Utricularia inflata,* as well as by *Leersia hexandra*, *Carex walteriana*, and *Echinodorus parvulus* that are submersed or shallowly emergent. In the zone of highest water level fluctuation, *Panicum languinosum*, *Panicum sphaerocarpon*, and *Panicum verrucosum* were dominant. *Rhexia virginiana* and *Rhexia mariana* were also present in this zone. Thus, the interior of the bay was developing floristic characteristics typical of an herbaceous meadow as described by De Steven and Toner (1997), with diagnostic species such as *Leersia hexandra*, *Eleocharis* spp., *Ludwigia sphaerocarpon* and *Rhexia* spp. Outside of the area that was ponded during the growing season, weedy upland species such as *Erichtites hieracifolia*, *Eupatorium* spp. and *Andropogon virginicus*, and vines such as

Smilax spp. and *Rubus* spp. dominated the bay. This zone also had the largest number of pine and hardwood tree seedlings. Rare or uncommon wetland plant species such as *Croton elliottii*, *Echinodorus parvulus*, *Iva microcephala*, and *Scleria reticularis* were found in the bay, and two of these four species (*Echinodorus parvulus* and *Iva microcephala*) were also found in the seed bank (see Chapter 2, this thesis). Bennett and Nelson (1991) found this depression meadow community type uncommon in Carolina bays in South Carolina, and it may occur more frequently on the upper Coastal Plain than elsewhere. De Steven (1994) lists the herbaceous meadow community as important because of the number of rare plant species found within it.

<u>Wetland site scores</u>

The wetland site scores seemed to be an effective measure of the change in wetland vegetation in Bay 93. We did not necessarily expect the different treatments alone to cause changes in wetland site scores, and they did not. The site score metric corresponded much more closely to the elevation and hydrologic gradients than to the treatments. The site scores were particularly useful in describing the changes in the clear-cut sections of the bay. The trend from 1994 to 1995 of lowering site scores illustrates the change toward wetter conditions and wetland plant community development at lower elevations within the bay.

In general, wetland site scores are one part of the evaluative process for restoration success. They are used to assist in determining potential credits for mitigation purposes. Vegetation is sampled at several points within the designated restoration area and scaled by the NWI. These scores are then averaged to give a wetland score for each location. A percentage of the locations sampled must qualify as having wetland vegetation in order for credits to be assigned (Marsh et al. 1996). Even though site scores are commonly used as a management tool in restoration projects, using site scores as a metric for wetland change is not a common practice in ecology. A number of studies have used site scores to characterize wetland vegetation (Michener 1983; Siegelquist et al. 1990; Atkinson et al. 1993), but in only one instance have we found a study that has used site scores to categorize wetland change along a gradient (Brown and Bedford 1997). In Bay 93, the site scores allowed for meaningful determination of wetland change, while still retaining a degree of detail that allowed us to examine that change across a gradient. The ability to link commonly used management techniques such as NWI classifications with processes such as development of hydrologic gradients should increase understanding of how evaluative tools and wetland processes are related.

Restoration implications

It has been demonstrated that Carolina bays and similar small, depressional wetlands are unique habitats that afford numerous animal and plant species a refugia in the oftentimes homogenously xeric upland habitats of the Coastal Plain pine forests (Sutter and Kral 1994; Semlitsch and Bodie 1998). As such, protection and restoration of these wetlands is of particular benefit to those who wish to maintain diversity on a landscape level.

The primary purpose of the restoration of Bay 93 was to evaluate methodologies that would maximize the effects of the hydrologic restoration in the initial years of the project. Through these efforts, it was our hope to establish reasonable goals and directions of future restorations in similar depression wetlands. Our conclusions are somewhat limited by the lack of replication in other bays, or replication within Bay 93, but our results are suggestive of the positive potential for bays as wetland restoration sites. Landowners need motivation for restoration, not only in terms of increased value of wetland habitats, but also through clear, cost effective pathways to attain a level of restoration success. This is especially important for small Carolina bays that exist as depressions that are located, in the majority of instances, on privately owned land. The initial response in Bay 93 demonstrates that if natural hydrologic patterns can be restored to drained Carolina bay wetlands, other low cost treatments such as removal of non-wetland trees and soil disturbance that take advantage of remnant seed sources can positively influence the development of wetland vegetation. In instances where *in situ* seed sources are not readily available more intensive restoration efforts such as transplanting soil or plants from similar wetland habitats may still be required (Galatowitsch and van der Valk 1996a). The effect of fire as a litter removal tool and seed germination cue was not found to be beneficial in Bay 93. However, fire may still play a role in the long-term successional development of plant communities in depression wetlands (Kirkman 1995; Kirkman et al. 2000). The disturbance associated with most Carolina bays is relatively simple, hydrologic alteration. Research in Bay 93 suggests that for the hydrologic and vegetation aspects of restoration, the simple treatments imposed were effective. More importantly, the presence of an *in situ* seed source allowed the wetland ecosystem to undergo natural processes of development and “self-design” once the hydrologic conditions were restored. Similar approaches have been used successfully in other freshwater wetland ecosystems where restoring the hydrology promotes recovery through natural successional (Mitsch and Wilson 1996).

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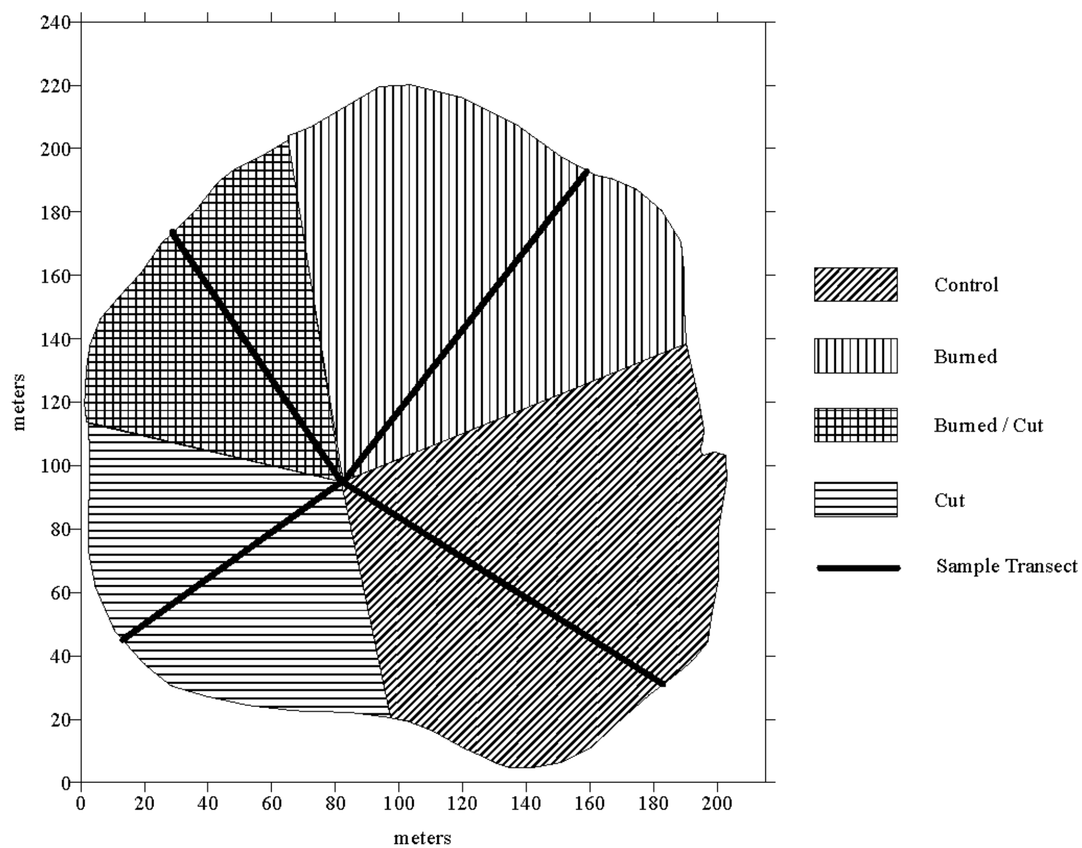


Figure 1. Carolina bay 93 separated into four treatment areas. Sample transects were randomly assigned within each treatment.

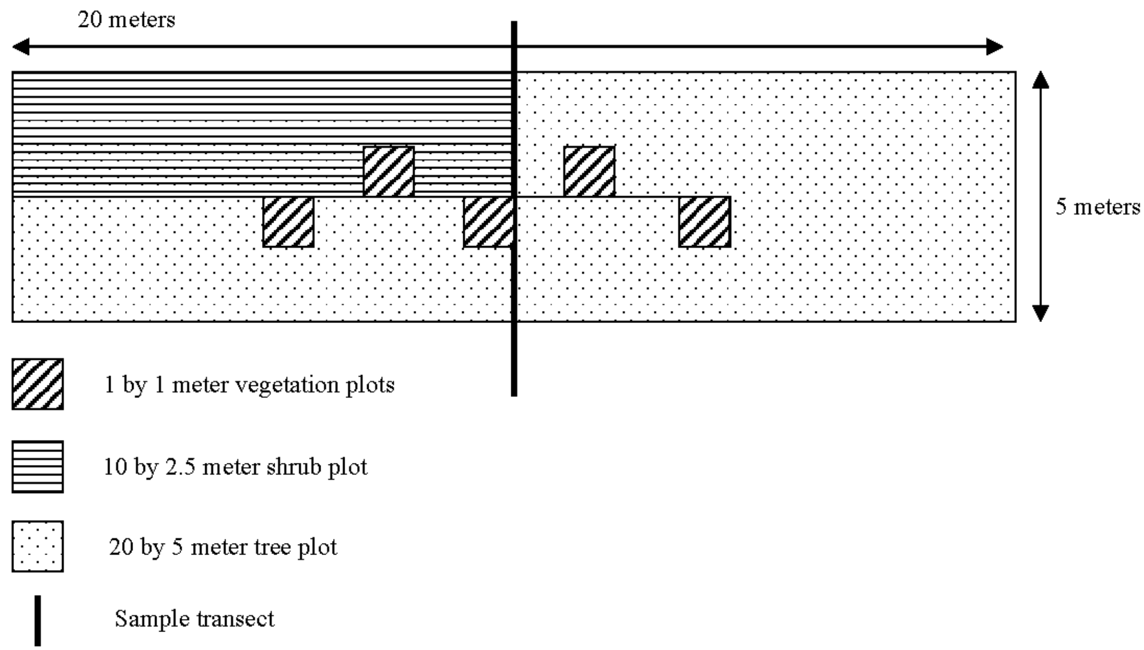


Figure 2. Schematic diagram of vegetation, shrub, and tree sampling design for one position along the sampling transect.

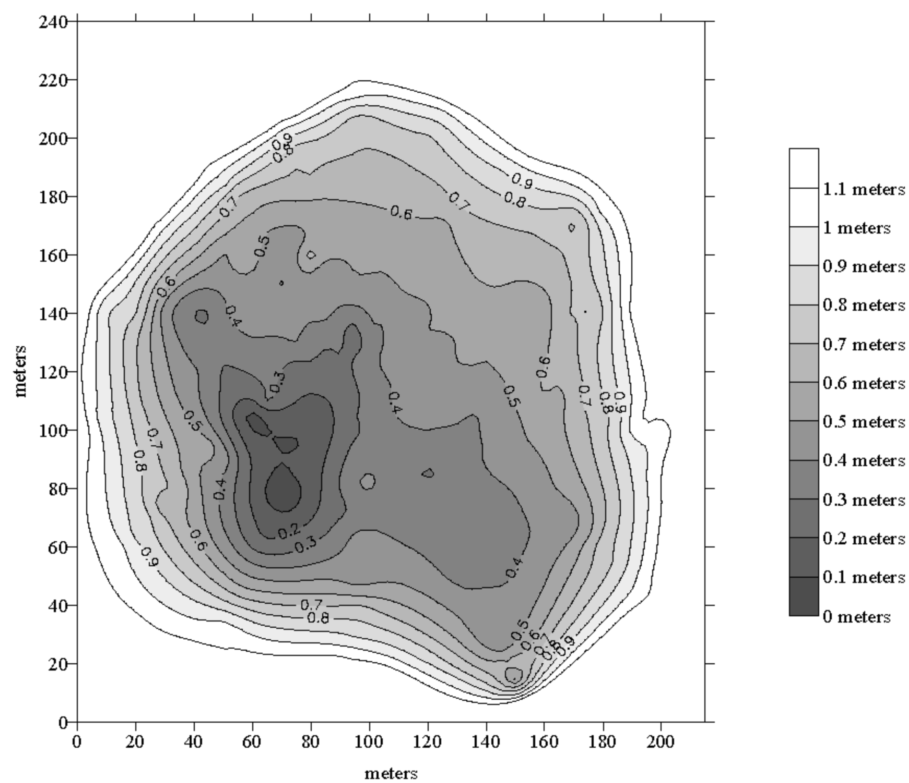
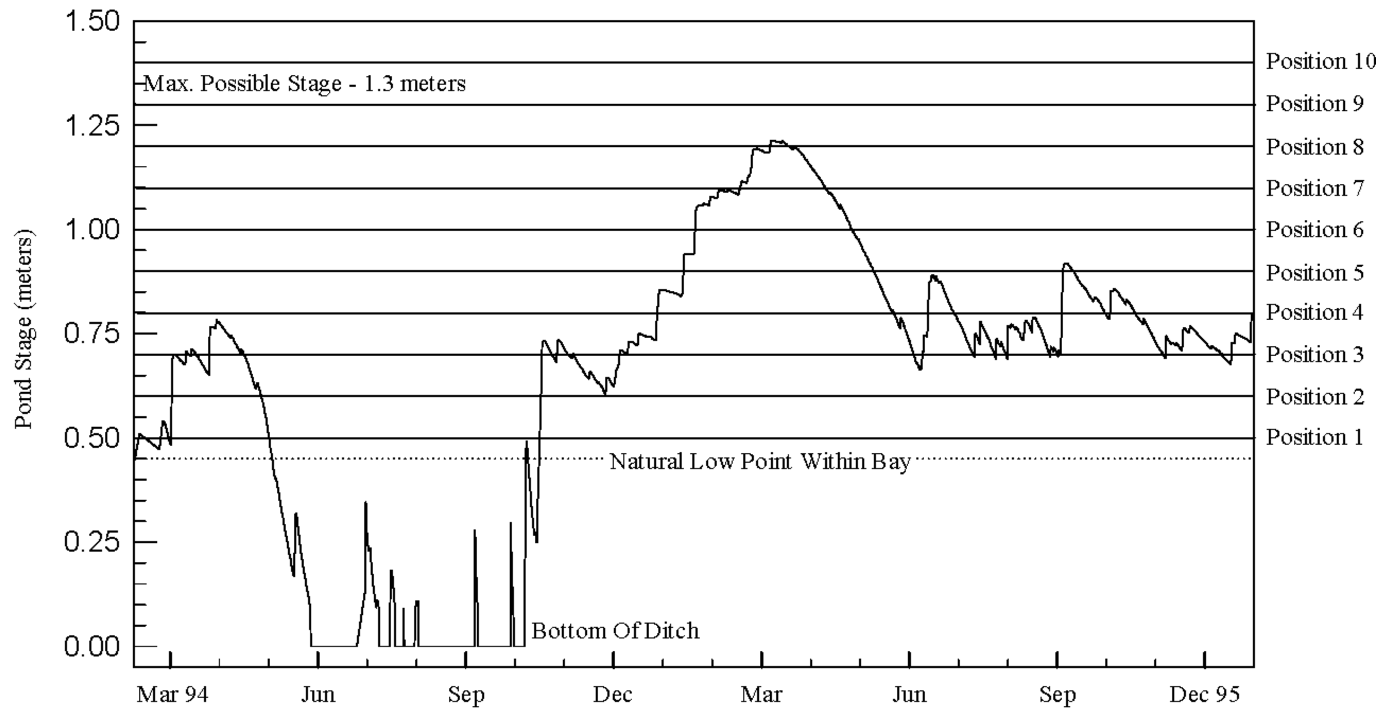


Figure 3. Topographic map of Bay 93. Contour lines are drawn at .1 meter intervals.



(7 Feb., 1994 - 24 Dec., 1995)

Figure 4. Bay 93 hydrograph with sampling points at the corresponding elevation position. The natural low point within the bay was .45 meters above the bottom of the ditch at the Stevens recorder. The ditch was closed in the fall of 1993.

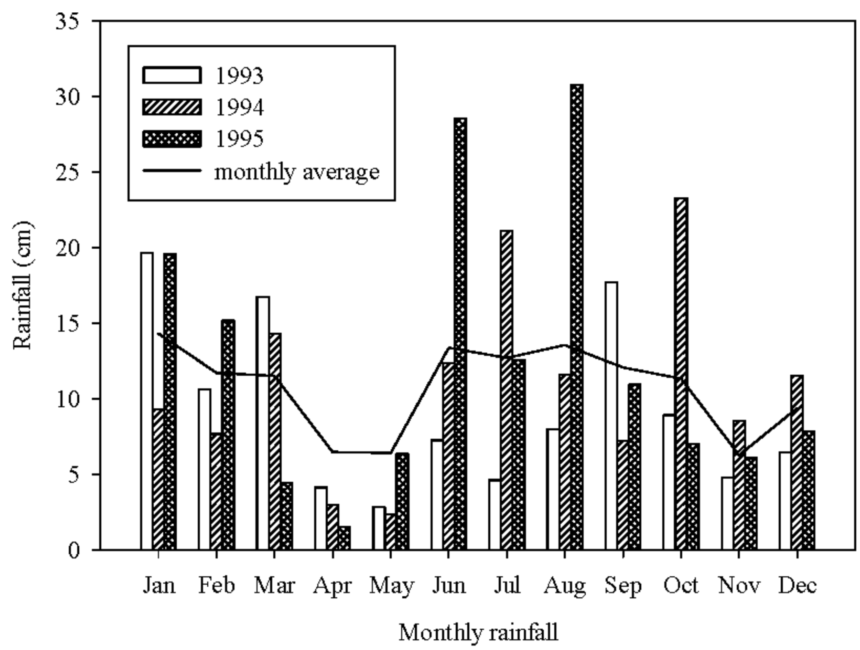


Figure 5. Monthly precipitation by year and average precipitation for Blackville 3W permanent weather station, Blackville, SC.

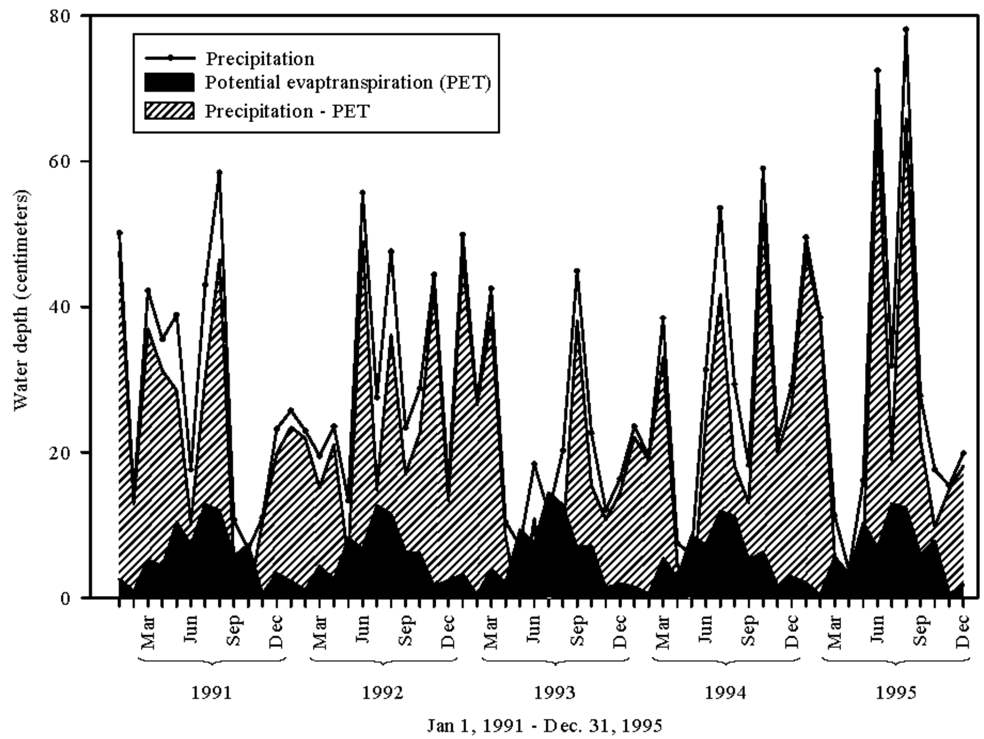


Figure 6. Precipitation, potential evapotranspiration, and difference for the years 1991 through 1995. After the ditch was closed in 1993, the difference in precipitation and evapotranspiration represented the principal components of the water budget for the bay.

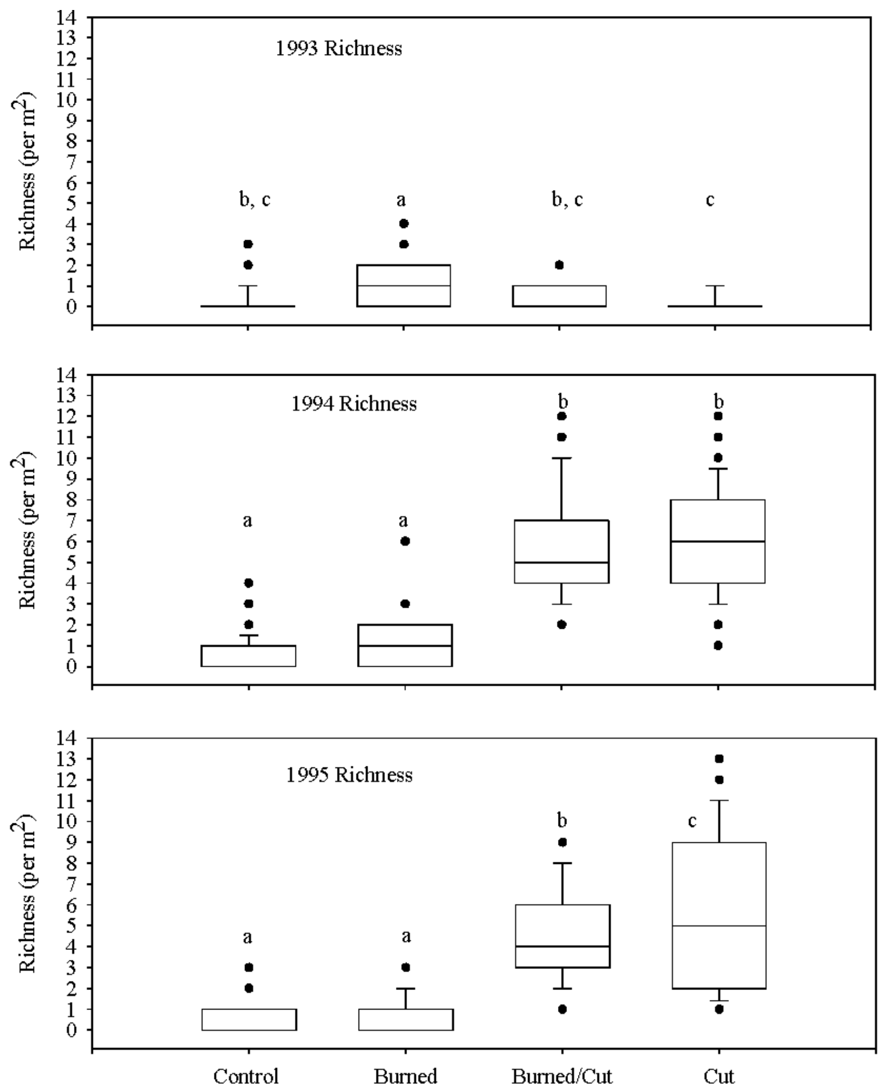


Figure 7. Box plots of species richness by treatment for 1993, 1994, and 1995. Box plots with different letters differ by treatment (Tukey's). Mean, 95% confidence intervals, and outliers are shown.

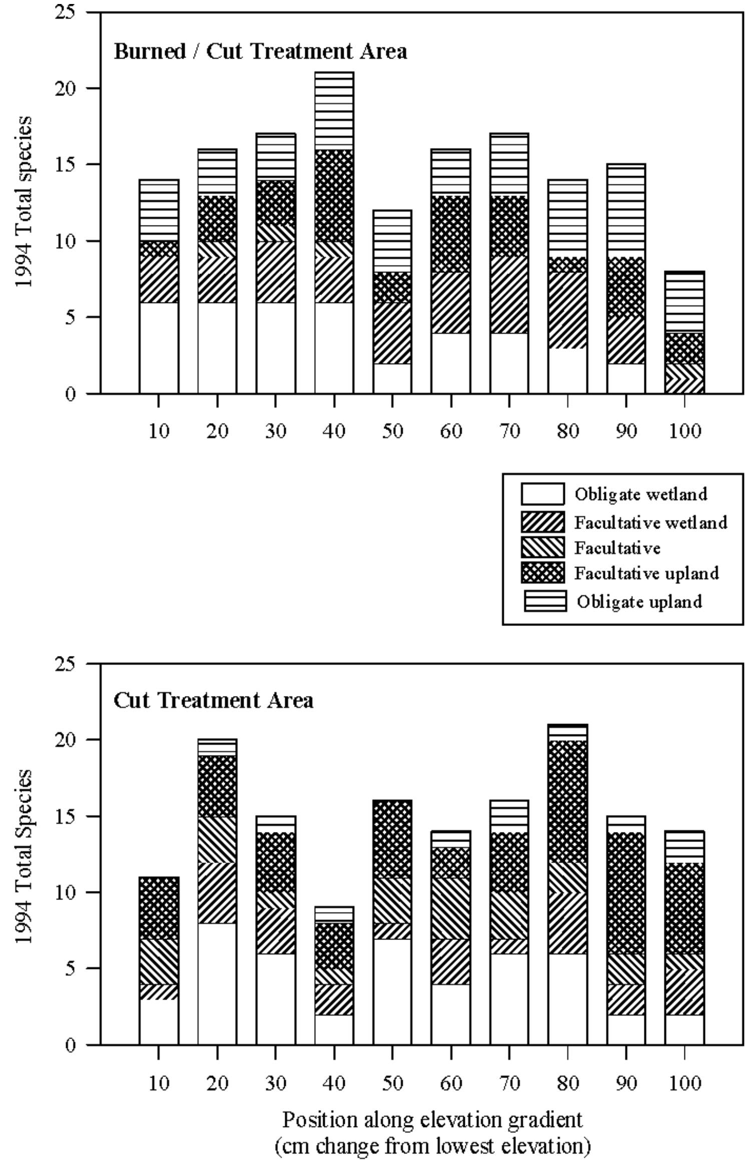


Figure 8. Total number of species by position along the elevation gradient separated into the appropriate National Wetland Inventory designation for clear-cut treatments in 1994.

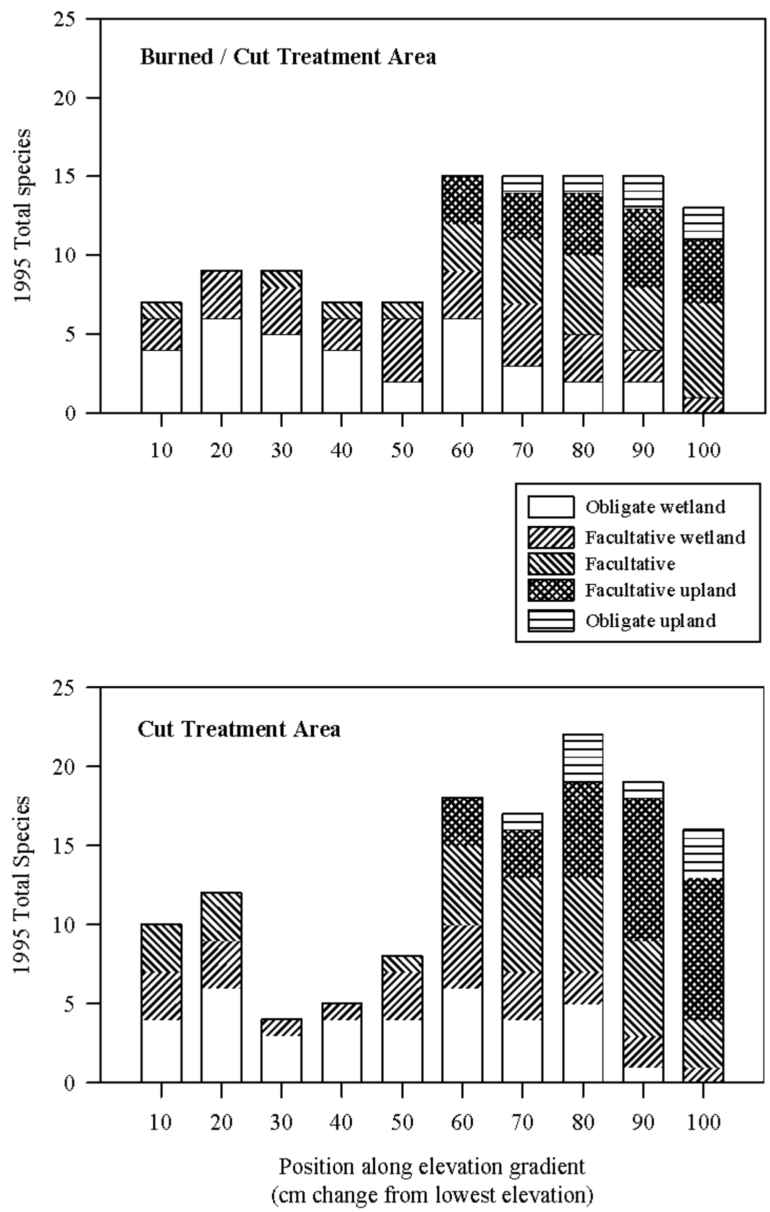


Figure 9. Total number of species by position along the elevation gradient separated into the appropriate National Wetland Inventory designation for clear-cut treatments in 1995.

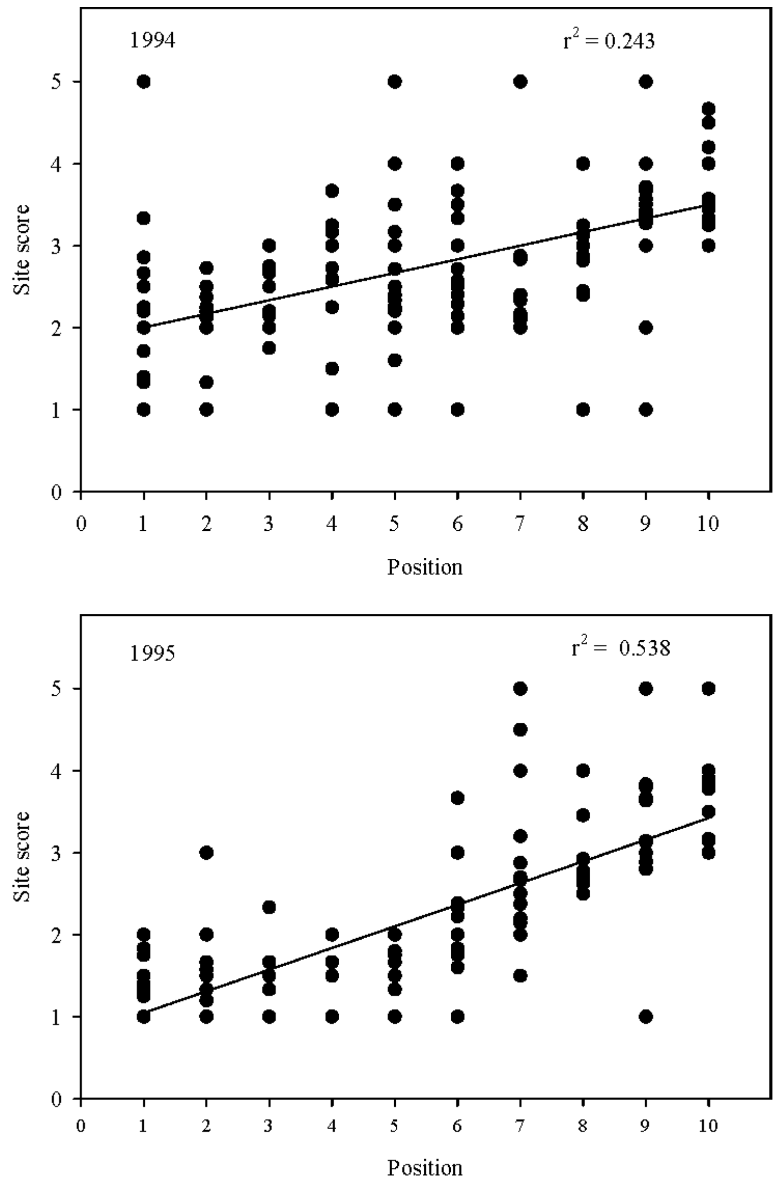


Figure 10. Correlation of wetland site scores with elevation for all treatments by year 1994 ($F = 51.25$, $p = .0001$) and 1995 ($F = 152.56$, $p = .0001$).

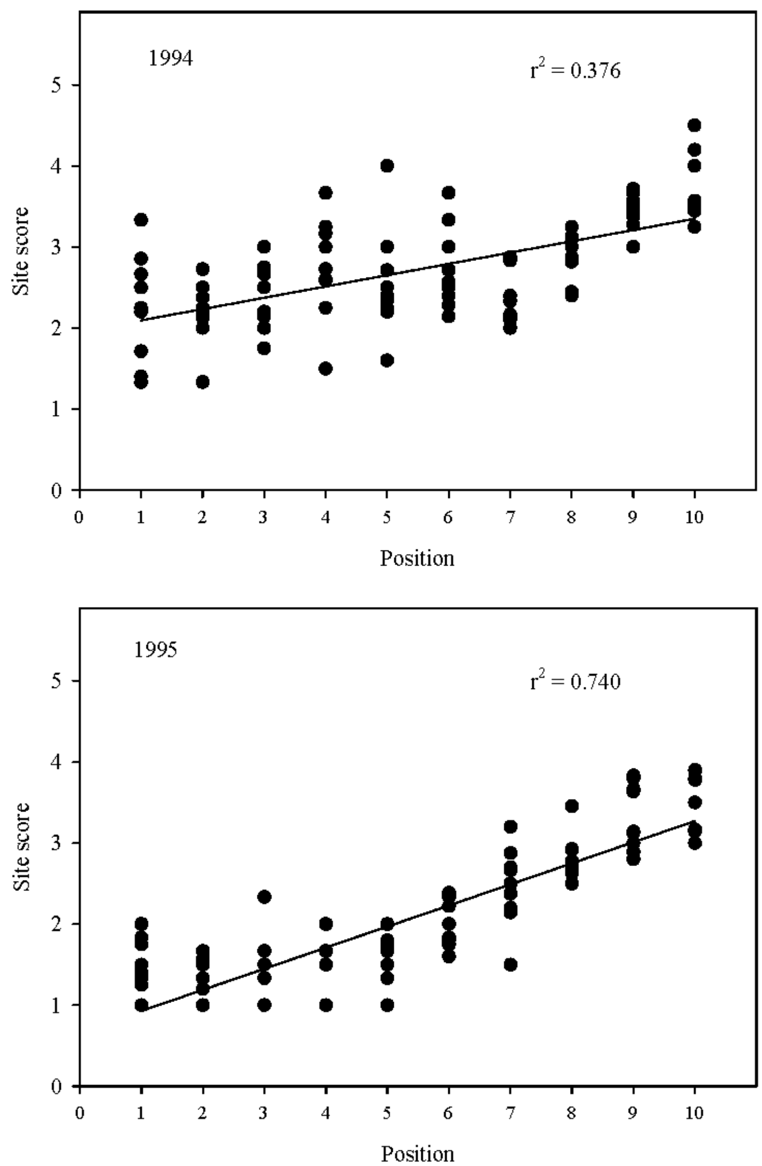


Figure 11. Correlation of wetland site scores with elevation gradient for clear-cut treatments by year 1994 ($F = 61.00$, $p = .0001$) and 1995 ($F = 288.16$, $p = .0001$).

Table 1. Total species richness for Bay 93 and each treatment within the bay by year.

Total Richness

	Control	Burned	Burned / Cut	Cut	Total
1993	6	9	7	3	12
1994	9	11	38	35	38
1995	7	9	38	44	52

Table 2. Species richness per m^2 for restoration treatments by year. Values with different letters indicate that richness differed by treatment for that year.

Richness per m2

	1993			1994			1995		
Treatment	**Mean**	**SE**		**Mean**	**SE**		**Mean**	**SE**	
Burned	1.04	0.14	a	0.92	0.16	a	0.42	0.11	a
Control	0.32	0.09	b,c	0.50	0.12	a	0.36	0.10	a
Burned / Cut	0.52	0.09	b,c	5.66	0.36	b	4.52	0.30	b
Cut	0.18	0.05	c	5.94	0.38	b	5.42	0.54	c

Table 3. ANOVA table for wetland site scores and species richness per m^2 for pre- and post-restoration treatments, position along the elevation gradient, and the interaction of the two factors.

	Treatment DF = 3		Position DF = 9		Treatment*Position DF = 18	
	F stat	Pr >F	F stat	Pr >F	F stat	Pr >F
Site score						
1993	4.45	0.0079	1.42	0.2091	3.46	0.0003
1994	0.78	0.5067	6.5	0.0001	1.64	0.0441
1995	0.63	0.5985	16.98	0.0001	1.57	0.0792
Richness						
1993	19.06	0.0001	2.69	0.0062	2.39	0.0004
1994	128.48	0.0001	0.96	0.4763	2.27	0.0009
1995	153.78	0.0001	15.73	0.0001	4.66	0.0001

Table 4. Percent cover of the ten species with highest density in 1994 and 1995 (16 species total) presented by year. The change in percent cover is significantly different at .05.

Percent cover (per m^2)

	1994		1995		change		Pr > t	
	Cut	**Burned / Cut**	**Cut**	**Burned / Cut**	**Cut**	**Burned /Cut**	**Cut**	**Burned / Cut**
Carex glaucescens	2.4	4.8	1.55	2.25	-0.85	-2.55	0.399	0.0777
Carex walteriana	1.5	0.65	8.82	1.35	7.32	0.7	0.0061	0.3979
Cyperus haspan	4.2	5.25	0.35	1.55	-3.85	-3.7	0.0056	0.0222
Cyperus retrorsus	4.35	6.9	0.55	2.7	-3.8	-4.2	0.0028	0.0006
Echinodorus parvulus	0	0	1.23	3	1.23	3	0.1653	0.1193
Erichtites hieracifolia	7.5	7.5	1.65	2.85	-5.85	-4.65	0.0199	0.0203
Eupatorium capillifolium	10.85	13.9	3.95	4.65	-6.9	-9.25	0.0009	0.0005
Iva microcephala	14.75	7.7	1.05	2.7	-13.7	-5	0.0005	0.0311
Juncus repens	0	0	3.45	5.85	3.45	5.85	0.0024	0.021
Leersia hexandra	0.3	1.2	5.3	4.65	5	3.45	0.0531	0.0151
Panicum languinosum	13.95	5.75	2.9	1.65	-11.05	-4.1	0.0002	0.0327
Panicum sphaerocarpon	2.45	5.15	6.65	4.85	4.2	-0.3	0.1342	0.09093
Panicum verrucosum	6.85	15.2	4.51	7.55	-2.34	-7.65	0.4133	0.027
Polypremium procumbens	4.4	2.4	4.5	1.5	0.1	-0.9	0.9388	0.3222
Rhexia mariana	4.2	3	10	3.3	5.8	0.3	0.0336	0.7846
Rhexia virginica	6.45	5.3	5	7.85	-1.45	2.55	0.347	0.1394

Table 5. Species richness per m^2 for position along the elevation gradient by year. Values with different letters indicate that richness differed by position for that year.

Richness per m^2

	1993			1994			1995		
position	**Mean**	**SE**		**Mean**	**SE**		**Mean**	**SE**	
1	0.40	0.11	a	3.00	0.51	a	1.85	0.43	a
2	0.20	0.09	a	3.25	0.82	a	1.75	0.45	a
3	0.20	0.09	a	2.95	0.76	a	1.10	0.27	a
4	0.55	0.15	a	3.15	0.87	a	1.10	0.26	a
5	0.40	0.13	a	3.20	0.60	a	1.45	0.37	a
6	0.75	0.19	a	3.30	0.62	a	3.50	0.82	b
7	0.45	0.14	a	3.30	0.83	a	3.80	0.84	b
8	0.65	0.18	a	4.00	0.88	a	4.40	1.06	b
9	0.70	0.22	a	3.80	0.79	a	4.35	0.90	b
10	0.85	0.26	a	2.60	0.53	a	3.50	0.75	b

Table 6. Means and standard error terms for wetland site scores for position along elevation gradient and treatment by year.

1993	**Control**		**Burned**		**Burned / Cut**		**Cut**	
Position	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1	4.00	.	3.00	0.00	3.75	0.25	4.00	.
2	.	.	3.00	.	.	.	1.00	0.00
3	.	.	3.00	.	4.50	0.50	1.00	.
4	4.00	0.00	3.33	0.33	4.00	.	4.00	0.00
5	3.00	2.00	2.16	0.44	4.00	0.00	.	.
6	2.83	0.17	3.88	0.13	4.00	0.00	.	.
7	.	.	3.40	0.40	4.00	0.00	.	.
8	4.00	.	3.50	0.29	3.00	0.71	.	.
9	4.50	0.50	3.67	0.21	3.00	.	.	.
10	5.00	.	3.77	0.15	3.00	.	2.00	0.00

1994	**Control**		**Burned**		**Burned / Cut**		**Cut**	
Position	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1	2.31	0.94	1.33	0.33	2.09	0.23	2.45	0.33
2	.	.	1.00	.	2.16	0.07	2.14	0.24
3	.	.	2.00	.	2.47	0.17	2.27	0.20
4	1.00	0.00	3.00	.	2.96	0.21	2.58	0.31
5	5.00	0.00	2.41	0.57	2.56	0.14	2.64	0.41
6	2.83	0.93	2.75	0.75	2.67	0.17	2.73	0.27
7	5.00	.	3.50	1.50	2.22	0.16	2.52	0.14
8	1.00	.	3.50	0.29	2.91	0.14	2.88	0.12
9	3.00	2.00	3.33	0.47	3.18	0.13	3.51	0.06
10	4.33	0.33	3.67	0.21	3.75	0.22	3.78	0.14

1995	**Control**		**Burned**		**Burned / Cut**		**Cut**	
Position	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1	2.00	0.00	.	.	1.33	0.12	1.60	0.14
2	.	.	2.50	0.50	1.34	0.11	1.21	0.13
3	.	.	.	.	1.47	0.24	1.10	0.10
4	.	.	1.00	.	1.77	0.10	1.10	0.10
5	.	.	.	.	1.83	0.07	1.31	0.15
6	2.88	0.48	1.00	.	1.88	0.11	2.06	0.13
7	2.00	.	4.50	0.50	2.25	0.20	2.68	0.18
8	.	.	4.00	.	2.70	0.03	2.89	0.16
9	2.33	2.31	3.88	1.02	3.20	0.16	3.38	0.20
10	4.33	0.33	4.00	1.00	3.32	0.14	3.65	0.17

Table 7. Means and standard error terms for wetland site scores along the elevation gradient by year.

Wetland site scores						
	1993		**1994**		**1995**	
position	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1	3.63	0.18	2.12	0.25	1.59	0.10
2	1.50	0.50	2.05	0.15	1.48	0.17
3	3.25	0.85	2.34	0.12	1.28	0.14
4	3.78	0.15	2.52	0.24	1.39	0.12
5	2.93	0.56	2.85	0.28	1.57	0.11
6	3.74	0.14	2.73	0.20	2.10	0.17
7	3.63	0.26	2.74	0.29	2.87	0.26
8	3.33	0.33	2.93	0.18	2.90	0.13
9	3.79	0.24	3.30	0.22	3.22	0.27
10	3.43	0.33	3.80	0.11	3.74	0.16

Table 8. Least square means and probability table for position by year (1994 and 1995). The positions are different at the .05 level.

1994 LS Means Pr > t

i/j	1	2	3	4	5	6	7	8	9	10	LS Means
1		1	1	0.6247	1	0.9657	1	0.0615	<.0001	<.0001	2.34
2	1		0.9995	0.3437	0.9955	0.7837	0.9962	0.01	<.0001	<.0001	2.26
3	1	0.9995		0.799	1	0.9956	1	0.1622	<.0001	<.0001	2.39
4	0.6247	0.3437	0.799		0.8853	0.9938	0.7598	0.9999	0.0509	0.0017	2.75
5	1	0.9955	1	0.8853		0.9994	1	0.2538	<.0001	<.0001	2.43
6	0.9657	0.7837	0.9956	0.9938	0.9994		0.9952	0.6218	<.0001	<.0001	2.56
7	1	0.9962	1	0.7598	1	0.9952		0.0669	<.0001	<.0001	2.41
8	0.0615	0.01	0.1622	0.9999	0.2538	0.6218	0.0669		0.0059	0.0003	2.85
9	<.0001	<.0001	<.0001	0.0509	<.0001	<.0001	<.0001	0.0059		0.5371	3.35
10	<.0001	<.0001	<.0001	0.0017	<.0001	<.0001	<.0001	0.0003	0.5371		3.73

1995 LS Means Pr > t

i/j	1	2	3	4	5	6	7	8	9	10	LS Means
1		0.9772	0.8034	0.9999	1	0.1203	<.0001	<.0001	<.0001	<.0001	1.53
2	0.9772		0.9994	1	0.7933	0.0001	<.0001	<.0001	<.0001	<.0001	1.33
3	0.8034	0.9994		0.99	0.477	<.0001	<.0001	<.0001	<.0001	<.0001	1.21
4	0.9999	1	0.99		0.9906	0.0344	<.0001	<.0001	<.0001	<.0001	1.42
5	1	0.7933	0.477	0.9906		0.4067	<.0001	<.0001	<.0001	<.0001	1.63
6	0.1203	0.0001	<.0001	0.0344	0.4067		0.0007	<.0001	<.0001	<.0001	2.03
7	<.0001	<.0001	<.0001	<.0001	<.0001	0.0007		0.5593	<.0001	<.0001	2.58
8	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.5593		0.0354	0.0006	2.81
9	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.0354		0.7347	3.24
10	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.0006	0.7347		3.53

Table 9. Mean differences and standard errors between 1995 and 1994 wetland site scores for all treatments by position along the elevation gradient.

Position	**Mean difference**	**SE**
1	-0.90	0.32
2	-0.36	0.38
3	-1.17	0.20
4	-1.24	0.24
5	-1.87	0.39
6	-0.73	0.32
7	0.30	0.70
8	-0.85	0.38
9	-0.08	0.43
10	-0.27	0.51

Table 10. Mean differences and standard errors between 1995 and 1994 wetland site scores for clear-cut (cut and burned/cut) treatments by position along the elevation gradient.

Position	**Mean difference**	**SE**
1	-0.81	0.18
2	-0.87	0.16
3	-1.09	0.20
4	-1.34	0.16
5	-1.03	0.23
6	-0.73	0.16
7	0.11	0.16
8	-0.10	0.15
9	-0.07	0.15
10	-0.31	0.15

CHAPTER 2:
SEED BANK CHARACTERIZATION AND CONTRIBUTION TO HERBACEOUS VEGETATION AFTER CANOPY REMOVAL AND BURNING TREATMENTS IN A CAROLINA BAY WETLAND

[1]Singer, J.S. and R.R. Sharitz to be submitted to *Wetlands*

Introduction

The seed bank, composed of all viable seeds that are in the soil and litter, is a repository for plant species. In dynamic ecological systems, the seed bank may be an *in situ* seed source that allows the vegetation to change when environmental change occurs. Environmental conditions may change on short-term temporal scales or long-term climatic scales, providing varying site conditions that may result in different species germinating from the seed bank into the extant vegetation.

Seed banks have been described as transient with seeds germinating within a year, or as persistent with seeds that may remain viable for extended periods of time (Thompson and Grime 1979). Although seeds of some wetland plants may survive for many years in the seed bank (Roberts 1970, 1981), the longevity of a diverse seed bank in wetland systems is questionable. Wienhold and van der Valk (1989) suggest that the majority of plants in prairie pothole wetlands have declining seed viability over time and that only 40% of wetland seeds survive in the seed bank after 20 years. The ability of seeds to remain viable for years after ideal conditions cease to exist, may have important ramifications during ecosystem restoration. Traditional restoration efforts focus on planting and/or using donor soils to inoculate a restoration area with species from a habitat similar to the target community (van der Valk et al. 1992; Vivian-Smith and Handel 1996; Brown and Bedford 1997). The presence of viable seeds of desirable species in the seed bank of the area to be restored would facilitate the restoration process and possibly eliminate the need for plantings.

In recent years substantial work has focused on seed banks and their importance in maintaining species richness as well in the vegetation over time (Baskin and Baskin

1998). Researchers have studied seed banks in a variety of ecosystems such as boreal forests, tundra, tropical forests, and temperate deciduous forests, and some of the most thorough studies have been conducted in wetlands (Leck et al. 1989). Most studies in wetland systems have shown that seed banks are important factors in understanding vegetation dynamics. In freshwater tidal marshes, work has concentrated on describing seed bank and vegetation patterns under fluctuating, but predictable hydrologic regimes (Leck and Simpson 1994, 1995; Leck 1996). Studies in prairie potholes of the upper Midwest and Canada have demonstrated that seed banks are fundamental in maintaining species richness in wetlands with unpredictable hydrologic conditions (van der Valk and Davis 1976, 1978). Seed banks in many wetlands also have been shown to be species rich. For example, Kirkman (1992) found that in four Carolina bay wetlands, the seed bank contained approximately twice the number of species as the extant vegetation.

Studies in wetland systems such as prairie potholes, show that the seed bank is important in the recovery of vegetation composition and structure during restoration (van der Valk 1981; Pederson and van der Valk 1984). Prairie potholes are abundant, small wetlands formed by glacial action, and their natural hydrology is influenced primarily by precipitation patterns. However, draining for agriculture or flooding to maintain waterfowl habitat has altered natural hydrologic patterns of many prairie potholes (Kadlec 1962). An altered hydrologic pattern changes the existing vegetation, the contribution of the vegetation to the seed bank, and also germination patterns from the seed bank. Because prairie potholes are important in terms of waterfowl habitat, there has been recent emphasis on protection or restoration of these systems (Poiani and Johnson 1989, 1993). Many prairie pothole restoration efforts involve simple changes in the drainage system to emulate pre-drained hydrologic conditions, and promote germination of wetland species from the seed bank (NAS 1992). Assessment of the ecological success of many of these restoration projects is still pending because of limited monitoring and poorly defined restoration goals and criteria (NAS 1992).

In many ways, Carolina bays of the southeastern Coastal Plain are similar to prairie potholes. Carolina bays are small and abundant depression wetlands. Their hydrologic regimes are influenced primarily by precipitation patterns, although there has been some recent evidence that groundwater may influence bay hydrology during wet periods in the climate cycles (Lide et al. 1995). Like prairie potholes, Carolina bays support emergent freshwater vegetation. The vegetation present in a bay at any one time is dependent on hydrologic conditions and may not represent the entire species richness in the wetland. Kirkman (1995) suggested that cyclical changes in the vegetation are expressed because of alternating periods of drought and higher rainfall. In particular, germination from the seed bank is influenced by hydrologic conditions that change over time. Collins and Battaglia (2001) found that hydrology acts as a filter for recruitment and species distribution in Carolina bays, and that bays with more stable hydrology are more likely to have zones of vegetation along the depth gradient.

Carolina bays tend to be more isolated on the landscape than prairie potholes, both spatially and hydrologically. Draining for increased agricultural production has hydrologically altered the majority of Carolina bays. In South Carolina, Bennett and Nelson (1991) estimated that agriculture, logging, or both have disturbed 97% of the Carolina bays. Unlike prairie potholes, these bays have not received a high level of protection or restoration effort. While a number of bays have been permanently altered by commercial or industrial development, many more bays have been disturbed to a lesser degree by draining and conversion to pasture and row crops (Bennett and Nelson 1991). The extent of disturbance may substantially influence the ease and effectiveness of restoration. If the seed bank remains intact, restoring the hydrologic conditions may be effective in re-establishing the natural vegetation dynamics of the bay. Furthermore, other restoration activities, such as removal of non-wetland vegetation, may enhance germination of wetland species from the seed bank.

Objectives

This study examines the effects of the seed bank on wetland vegetation development in a drained Carolina bay wetland in which the hydrology was restored. Through germination studies in the greenhouse and corresponding field vegetation sampling, the contribution of the seed bank to the initial wetland vegetation response was assessed. Specifically, the goals of the study were:

1. To analyze the content of the remnant seed bank after more than forty years of altered hydrology in order to determine if wetland species were present.
2. To determine if restoration treatments imposed on the bay affected the germination of wetland species in the seed bank.
3. To examine the spatial distribution of seed bank species germinating into the bay.

Methods

Study site

Carolina Bay 93, a 4.25 ha depressional wetland located on the U. S. Department of Energy's Savannah River Site in Barnwell County, South Carolina, was chosen as a wetland restoration site in the early 1990's. From 1949 and 1951 aerial photography, it appeared that the bay once supported herbaceous wetland vegetation. It was also evident from these photographs that the bay had been ditched prior to 1951. In the four decades since, the bay had become forested and was dominated by non-wetland, woody vegetation with a very small non-wetland herbaceous component.

In the summer of 1993, topographic data were gathered with a laser level at 5 m intervals along transects radiating from the center of the bay. The resulting depth measurements were used to generate a topographic map with a krieging program (Surfer; Golden Software 1999). The bay was found to be geomorphologically asymmetric, with the deepest point offset from the geographic center (Figure 1). Using the topographic map, the bay was divided into four radial quadrants, each of which included the entire depth gradient from the deepest point to the outside rim of the bay.

Vegetation

A randomly placed transect running from the center of the bay to the rim was established in each of the quadrants (Figure 1), and sample points were placed at 10 cm elevation intervals along each transect. The result was ten positions representing the depth gradient from the deepest point in the bay to the outside edge. At each of the ten positions, five 1 m^2 plots were established along a line perpendicular to the transect in order to sample the herbaceous vegetation (Figure 2). Additional plots were established on each transect at the center of the bay to sample in the deepest area. Vegetation was sampled in each of the 1 m^2 plots in 1993, 1994, and 1995. Density and percent cover were determined for each species for other analyses (Chapter 1), however, presence / absence data were used in the following comparisons with the seed bank.

Treatments

In September 1993 the ditch draining the bay was filled with an earthen dam equipped with a PVC drain that allowed for some control of the water level in the bay. Treatments that consisted of removal of all woody vegetation and prescribed burning were applied in order to achieve different conditions in each quadrant of the bay as follows: 1. The control received no treatment 2. One quadrant was burned. 3. One quadrant was clear-cut and burned. 4. One quadrant was clear-cut (Figure 1). Logging occurred during November 1993 and burning in January 1994. All woody stems were cut in the clear-cut quadrants. Trees of marketable size were removed from the bay, but excess coarse woody debris from de-limbing the timber was left in the bay.

Seed bank

Samples from the seed bank were collected immediately after the final burning treatment in January 1994. Ten sub-samples were collected at random locations within a 5 by 20 m plot at alternate vegetation sampling positions along the transect for each treatment, including the deep center position (Figure 2). The seed bank plots were perpendicular to the transect and centered on the position point on the sample transect. An eight-centimeter diameter soil sampler was pushed to a depth of 7 cm into mineral soil to obtain a sub-sample. These ten sub-samples from each plot were pooled and well-mixed, making six total samples per transect. Therefore, there was no replication of treatment and postion combinations for the seed bank experiment.

Rhizomes were removed from the soil and the seed bank samples were cold stratified for one month immediately after collection. Following the emergence method, samples were exposed to two germination conditions. Each sample was halved and each half spread over 3.8 cm of pine bark potting soil in 25 cm by 35 cm pans. One pan was kept inundated in 3 to 5 cm of water. The second pan of each sample was subjected to moist conditions in drained soil that was saturated every 3 to 5 days. All pans were arranged randomly on a greenhouse bench and allowed to germinate from February through May 1994, at which time almost all germination had ceased. The seedlings were identified, tallied and removed as they germinated. Seedlings that could not be identified were allowed to grow until a positive identification could be made. All species germinating from the seed bank were assigned to their national wetland indicator status (NWI) for plants in the Southeast (Reed 1988).

Statistical Methods

All analyses were performed with SAS V. 8.0 (SAS 2000) on the positions sampled within the bay. Presence / absence data on identified individuals within vegetation plots were used to estimate similarity to the seed bank. Jaccard's index of similarity, calculated as J_{index} = species in common / total species, was used to determine the similarity between the composition of the seed bank and the vegetation for every seed bank sampling position within each treatment, and for all positions within the entire bay. Non-parametric Kruskal-Wallis tests were used to examine differences between seed bank and vegetation similarity coefficients. PROC GLM was used to test whether restoration treatment, location, or their interaction influenced either mean species richness or mean seed abundance. For the description of persistence of seed bank species within the bay, the vegetation at each of the ten sampling positions was compared to the entire suite of species germinating from the seed bank, not just those germinating from any one seed bank sampling position or transect. All statistical results are reported on herbaceous species identified to the species level of detail unless noted otherwise. *Rubus* spp., present in the seed bank, was excluded from the analysis. Woody species, although included in tests on treatment and position effects, were excluded in the computation of similarity coefficients.

Results

The seed bank in Bay 93 was generally depauperate, with a total of 29 species found in the entire germination study. Of these, only three were woody species. *Myrica cerifera*, *Callicarpa americana*, and *Rhus copallina*, all understory shrubs, germinated in low numbers in the saturated treatment. No vine species germinated from the seed bank. Thus, the majority of the seed bank species were herbaceous, and all but three germinated in the saturated greenhouse treatment. The species that germinated under flooded conditions, *Echinodorus parvulus*, *Juncus repens*, and *Leersia hexandra,* are designated as obligate wetland species on the national list of wetland plants (Reed 1988). Six additional obligate wetland species germinated under saturated soil conditions: *Carex glaucescens*, *Cyperus haspan, Eleocharis obtusa*, *Fimbristylus autumnalis*, *Rhynchospora rariflora*, and *Viola lanceolata*. Grouped by NWI status, there were more obligate wetland species than any other designation in the seed bank (Figure 3). *Cyperus polystachos* and *Iva microcephala* were the only facultative wetland species that germinated. Additionally, *Echinodorus parvulus* and *Iva microcephala* are on the South Carolina threatened species list and as such are species of particular interest.

Seed density within the seed bank was also low, and there was no pattern of density across the elevation gradient. The highest density was found at the penultimate position of the burned treatment area (density = 403 seeds per m^2, Table 1). The variability between positions was high (Table 1), with the lowest density (21 seeds per m^2) at the penultimate position of the cut treatment area. The distribution of seeds analyzed by both species richness (DF = 3, F = .57, p = .6375, Table 2) and seed abundance (DF = 3, F = .20, p = .8968, Table 2) did not differ between treatment areas in Bay 93. The uniformity of seed distribution was also evident from the lack difference between positions within the treatments for richness (DF = 5, F = 1.74, p = .1637, Table 2) and abundance (DF = 5, F = .39, p = .8495, Table 2) along the elevation gradient. There was no interaction between these non-significant factors (Table 2) for richness or abundance. Although the seed bank was not correlated statistically with elevation across the bay, the high standard deviation suggests that the seeds were not evenly distributed horizontally within the bay.

Jaccard's index of similarity was used as an indicator of similarity in species composition between the seed bank and the extant vegetation. The coefficients were calculated at the position, treatment, and entire bay scales in an effort to fully evaluate how well the seed bank compared to the extant vegetation. The coefficients calculated at the position level showed how dissimilar the seed bank and the vegetation were in all treatments. In 1993, there was almost no similarity between the seed bank and extant vegetation (Table 3). Accordingly, there was no association between similarity and elevation (Table 3). At that time there was very little herbaceous vegetation sampled in any of the treatment areas, and the seed bank actually had higher species richness than the herbaceous vegetation (seed bank, 26; vegetation, 6). There were only two species sampled in the vegetation that were also present in the seed bank, *Hypericum hypericoides* and *Panicum scoparium.* In only two positions was a species that germinated in the seed bank also sampled in the extant vegetation. In these two positions, *Panicum scoparium* was present in the seed bank and in the vegetation plots.

By 1994 the vegetation in the burned / cut and cut treatment areas was beginning to develop greater numbers of species. This was potentially due to the clear-cutting and consequent disturbance of the soil promoting germination from the seed bank. Similarity between the seed bank and vegetation in the control and burned treatment areas remained low, although there was a similarity coefficient of .33 for position 4 in the burned area. Only three species were sampled in the vegetation at this position, and *Panicum scoparium* was found in both the vegetation and seed bank. The burned / cut and cut treatment areas showed similarity coefficients ranging from 0 to .33, and there were few completely dissimilar locations. Most similarity coefficients ranged between .15 and .25 in these two clear-cut treatments. There was no pattern of similarity associated with position along the depth gradient (Table 3). The highest coefficient of similarity was located at the highest elevation (.33) in the cut area, while the lowest coefficient (0) was in the highest elevation of the burned / cut treatment area.

Jaccard's similarity coefficients were generally lower for all positions in 1995 than in 1994, but still much higher than those in 1993. By 1995 the water levels in the lower elevations of the bay were higher for longer periods of time, lowering the species richness of the vegetation at those locations. This decrease in richness is reflected in the similarity coefficients of the lower positions in the burned / cut and cut treatment areas (Table 3). The coefficients for the lowest position remained essentially the same as in 1994, but they dropped at positions 2 and 3. Coefficients for positions 6 through 10 changed slightly from 1994 to 1995, but no pattern of increase or decrease in similarity between seed bank and vegetation with regard to elevation was apparent (Table 3).

Analysis of Jaccard's similarity coefficients irrespective of position along the depth gradient further illustrates the increase in similarity between species expressed from the seed bank and extant vegetation in the two clear-cut areas (Table 4). At the treatment level, the differences between similarity of seed bank and vegetation are significant for both 1994 and 1995 (Table 4). The highest similarity is in the burned / cut treatment area in 1994 (.44). The slight drop in similarity in 1995 may be attributed to the increased water levels at lower elevations limiting the species richness at those locations. There is a gradual increase in similarity as the scale at which the similarity coefficient is calculated increases. For total richness across the entire bay, more than half of the extant species sampled were found in the seed bank (.51) in 1994 (Table 5). By 1995, the total similarity had decreased to .48, but was still higher than coefficients calculated at the position or treatment levels.

Species found in the seed bank persisted in the sampled vegetation from 1994 through 1995. Of the nine obligate wetland species found in the seed bank, six were present in the vegetation in 1994 and seven by 1995 (Figure 3). *Juncus repens* and *Echinodorus parvulus* were not sampled in 1994, but appeared in the wetter portion of the bay in 1995. One obligate wetland species from the seed bank, *Rotala ramosior*, was sampled in 1994, but was not found in 1995. All other seed bank species that appeared in the vegetation in 1994 persisted through 1995. The seed bank may have been important in establishing species in the restoration treatments that demonstrated the greatest vegetation response. More than half of the plant species sampled in the burned / cut and cut treatment areas in 1994 were ones found in the seed bank (Figures 4 and 5).

For both clear-cut treatments, the numbers of species from the seed bank were relatively uniform across the elevation gradient. The highest position along the gradient in the burned / cut area had the lowest number of species germinating from the seed bank, but also the fewest total species. Some plots at this location were covered by large amounts of coarse woody debris that decreased the amount of exposed soil surface available for germination of seeds from the seed bank or dispersal. Other species transported into the bay from outside sources by wind, animal, or bird transport also formed a substantial portion of the vegetation sampled within the bay. By 1995, as hydrologic changes began to sort species along the elevation gradient, the number of seed bank species sampled in most locations decreased (Figures 4 and 5). However, the total richness of seed bank species sampled within the bay actually increased by one obligate wetland species.

Discussion

There is evidence from the seed bank and vegetation data that the seed bank was a potential source of plant species in the restoration of Bay 93. The number of species found in the seed bank does not compare favorably with seed banks in other, less disturbed, depression wetlands, however. Kirkman (1992) sampled 107 taxa in the seed banks of several small Carolina bays located within 24 kilometers of Bay 93. The densities of seedlings germinated from the seed banks of these bays were also far greater (>72,000 per m^2) than those found in Bay 93 (highest density of 403 per m^2). The wetlands in Kirkman's (1992) study were chosen because they were relatively unimpacted and exhibited highly variable hydroperiods. Under such variable conditions, a large seed bank may develop. Alternately, Poiani and Dixon (1995) found only 16 to 35 species per bay in the seed banks of seven bays in South Carolina using similar sampling techniques. Also, McCarthy (1987) found low numbers of species in intermittently flooded ponds in New Jersey, but the density of seedlings was still high (17, 943 per m^2).

The low seed density found in Bay 93 is may be typical of seed banks in other wetlands subjected to altered hydrology. Wienhold and van der Valk (1989) found that viable seed density dropped dramatically thirty to forty years after draining occurred in several prairie pothole wetlands in the Midwest. They found an average viable seed density of 106 seeds per m^2 after 40 years of drainage, which is similar to the mean density of 143 seeds per m^2 sampled in Bay 93. Wienhold and van der Valk (1989) did see variation in seed densities in prairie potholes in different Midwestern states, suggesting that factors across the range of these wetlands or climatic differences have an impact on seed viability over time. Seed persistence in the soil depends on several factors. Pathogens, aging, and seed predators are the primary cause of seed mortality in the soil (Baskin and Baskin 1998). Testing the longevity of seed viability is inherently experimental. Only recently has it been possible to radiocarbon date and germinate the same seed due to the amount of material required for the radiocarbon dating. Ongoing experimental studies have shown seeds germinating 6 to 100 years after burial in natural conditions for known periods of time (Baskin and Baskin 1998). Other germination studies from archeological sites with seeds of inferred age have estimated seed longevity of thousands of years, albeit at reduced viability (Simpson et al. 1989).

Even though the seed bank in Bay 93 was depauperate, it was potentially vital in establishing vegetation in the bay after restoration treatments were imposed. The lack of whole bay replication, due to the constraints of the project, limits the degree to which conclusions made here can be extrapolated. It is important, however, that wetland species were present in the seed bank, germinated into the bay, and remained in the extant vegetation for the duration of the study. The degree to which seeds from other sources may influence the initial vegetation response after restoration needs to be examined more closely. Seeds entering the bay from outside sources were predominantly non-wetland species that could have been associated with the surrounding planted loblolly pine upland community. Poiani and Dixon (1995) demonstrated that the distance to upland clear-cuts was correlated with the number of weedy upland species found in the seed banks of seven Carolina bays, suggesting a potential influence of surrounding upland vegetation on the vegetation in Bay 93. The potential for Bay 93 to become dominated by weedy upland species was mitigated by the rapid development of wetland plants that were present as viable seeds in the remnant seed bank. Galatowitsch and van der Valk (1996) suggested that for isolated wetlands, such as prairie potholes, the seed bank was important in developing shallow emergent vegetation zones, especially for species with seeds not dispersed by wind or waterfowl. Germination of seeds from within the wetland was paramount to the development of wetland vegetation in restoring these wetlands. Alternate means of quickly establishing wetland vegetation, such as planting species and using donor seed banks are more expensive methods of restoration (van der Valk et al. 1992; Vivian-Smith and Handel 1996; Brown and Bedford 1997).

The life-history characteristics of species within the seed bank and the extant vegetation reveal patterns of recruitment and vegetation development within the bay. There were similar numbers of annual and perennial herbaceous species sampled in the seed bank (12 annual, 14 perennial, Appendix 1). There were more perennial species than annual species found in the extant vegetation for both 1994 (31 perennials, 19 annuals) and 1995 (28 perennials and 17 annuals). This suggests that perennial species, once established, may persist vegetatively without producing seed. In certain portions of the clear-cut treatment areas, *Carex walteriana,* a perennial, increased in cover more than any other species (Chapter 1, this thesis), suggesting that it was out-competing less hardy annual species by 1995. Kirkman (1992) found similar patterns of seed bank recruitment and subsequent dominance by strongly competitive perennials after soil disturbance. Many of the perennials found in Bay 93 were upland species that persisted at higher positions along the elevational gradient.

Contrary to findings from many other wetland systems (Keddy and Reznicek 1982; Leck 1989; van der Valk and Pederson 1989), the seed bank in Bay 93 was as much as 51% similar in comparison to the extant vegetation. The clear-cut restoration treatments had the greatest impact on vegetation development as well as seed bank germination. The clear-cutting treatment disturbed the soil, increased light levels, and may have increased temperature ranges. Seeds at or below the surface of the soil cannot germinate unless light, soil moisture, and temperature are not limiting factors (Baskin and Baskin 1998). The lack of red and blue light, coupled with relatively high levels of far-red light, effectively limit germination of many species under a canopy (Smith 1994). Removing the canopy provided unfiltered light that may have stimulated germination.

Wetting and drying, daily temperature fluctuations, and heat from fires are all environmental factors that can break physiological dormancy (Baskin and Baskin 1989). Each of these conditions resulted from the clear-cutting treatments imposed in Bay 93, and may have served to facilitate seed bank germination. Also, soil disturbance associated with the logging of the bay may have brought buried seeds associated with earlier wetland community types to the surface, where they germinated under more favorable wetland conditions.

The burning treatment had no noticeable effect on germination from the seed bank. However, the burning treatment was performed after the overstory was removed As a result, burning in the burned /cut treatment was patchy, and some areas were not burned down to mineral soil. It is possible that temperatures of the fire were not hot enough to stimulate germination in some species. However, the lack of germination in the burned treatment, where burning down to mineral soil did occur, suggests that canopy removal was more important in stimulating seed germination.

The degree of similarity between the seed bank and vegetation, coupled with the low densities of seeds in the soil, is somewhat paradoxical. The sampling technique seems to have been effective in sampling for species richness, especially in light of the number of wetland species germinating from the seed bank. There is a demonstrated tendency of underestimation of seeds in the soil using the emergence method (Poiani and Johnson 1988; Gross 1990; Brown 1992). Conditions necessary for the germination of all seeds are difficult to accommodate in a greenhouse study. In Bay 93, the seed bank richness and abundance were relatively homogenous across the elevation gradient within the wetland. Thus, the seeds in the seed bank experienced a variety of site conditions across the restored hydrologic gradient, increasing the probability that necessary conditions for germination would be met.

Recruitment from the seed bank was apparent in the first year after the restoration treatments were imposed. As the water levels in the bay increased, species associated with wetter habitats tended to remain in the deepest portions of the bay, while upland species dropped out of the lower elevations (Chapter 1). Collins and Battaglia (2001) found similar patterns in six intact Carolina bay wetlands in South Carolina. The restoration ramifications of this pattern are that if viable seeds of wetland species are present in the seed bank, it may be possible to manage for those species by restoring the hydrology and creating conditions that promote their germination and establishment.

Acknowledgements

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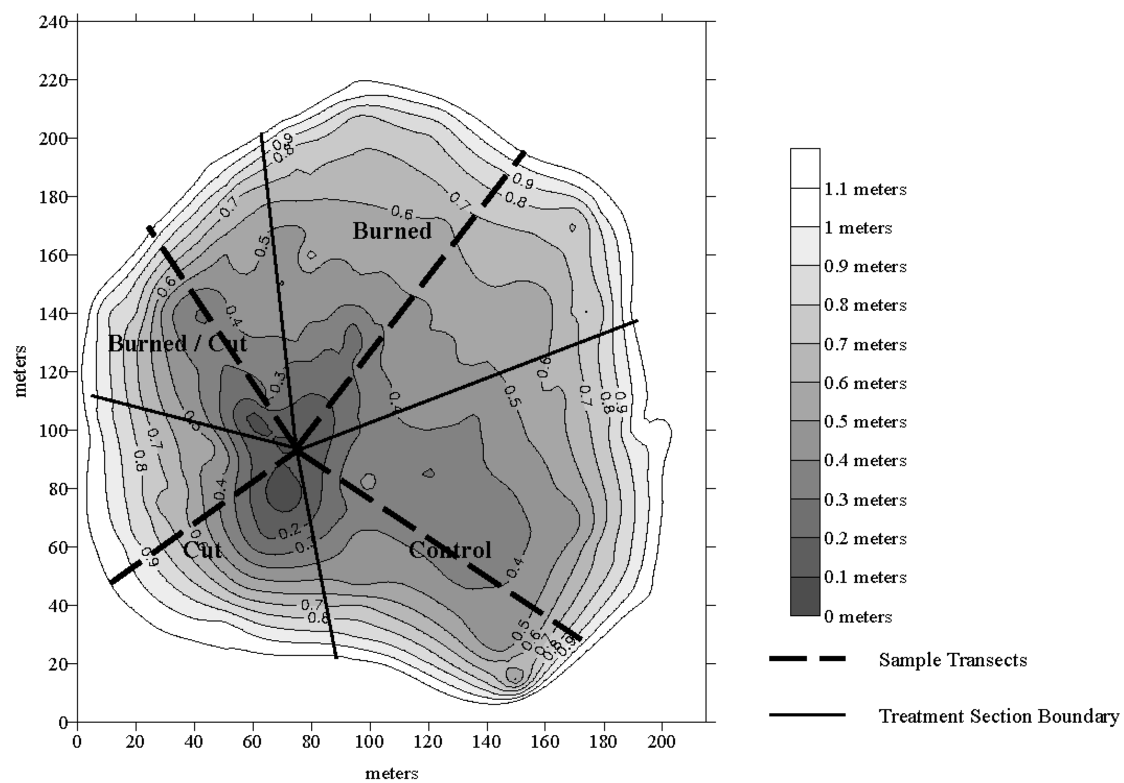


Figure 1. Topographic map of Bay 93 with treatments and sample transects. Contour lines are drawn at .1 meter intervals.

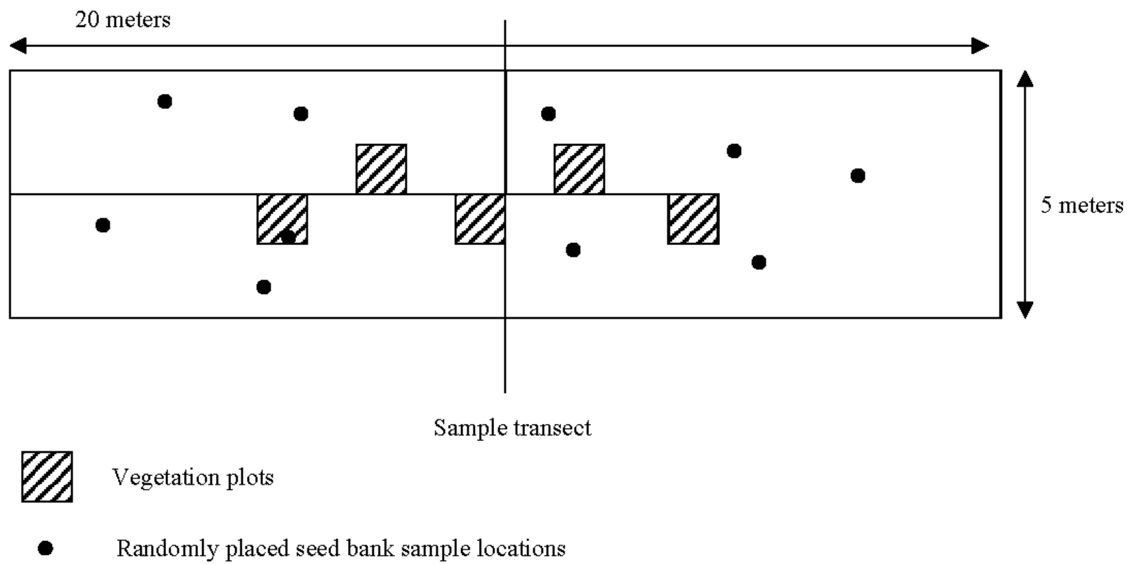


Figure 2. Seed bank and vegetation sampling design for one position along a sample transect.

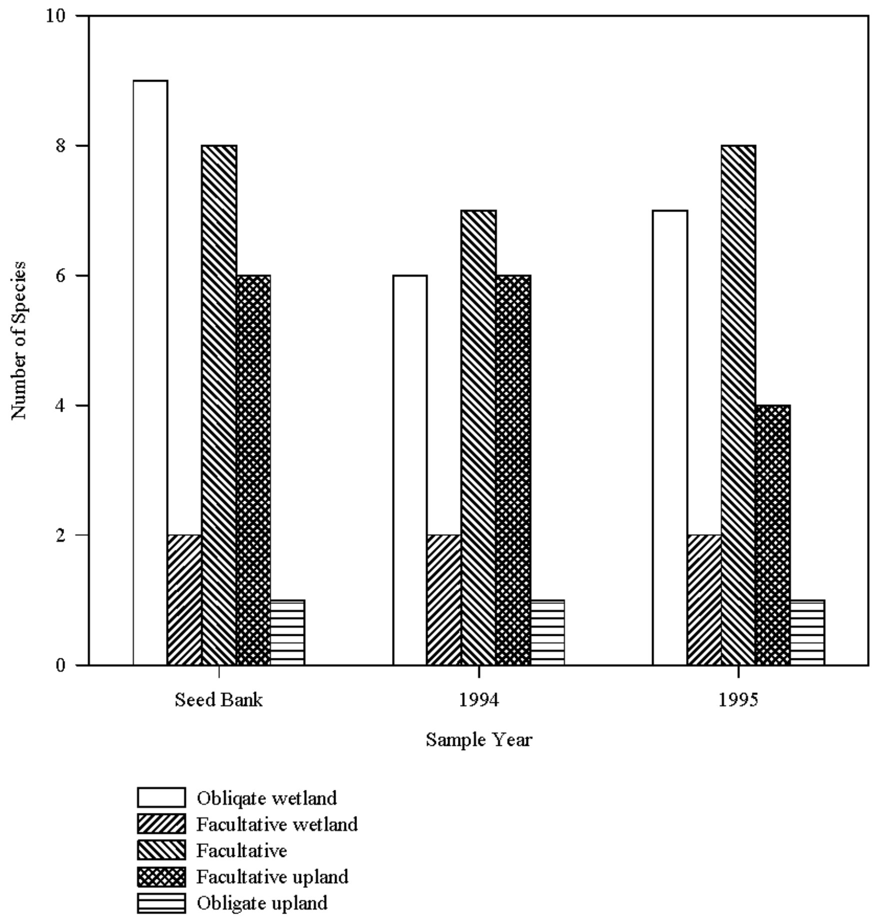
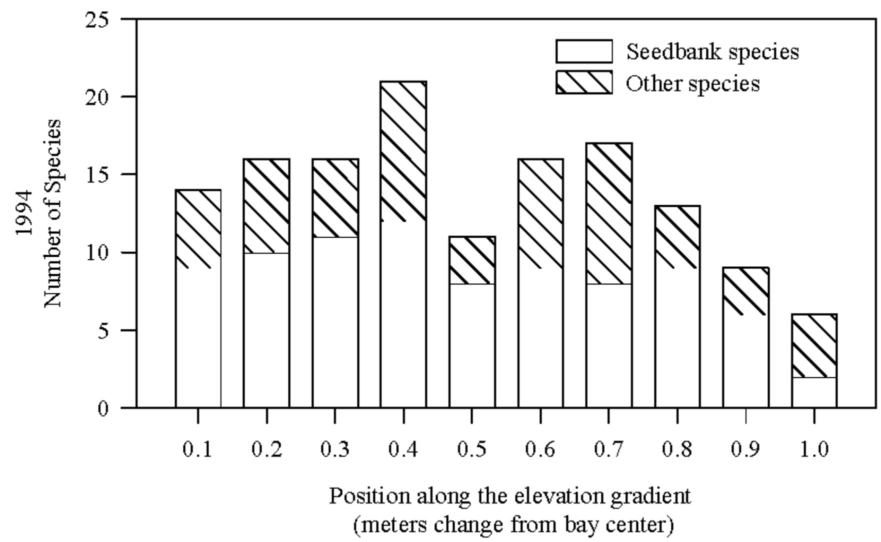


Figure 3. Seed bank (first set of bars) and seed bank species sampled in extant herbaceous vegetation, by year and national wetland indicator (NWI) status.



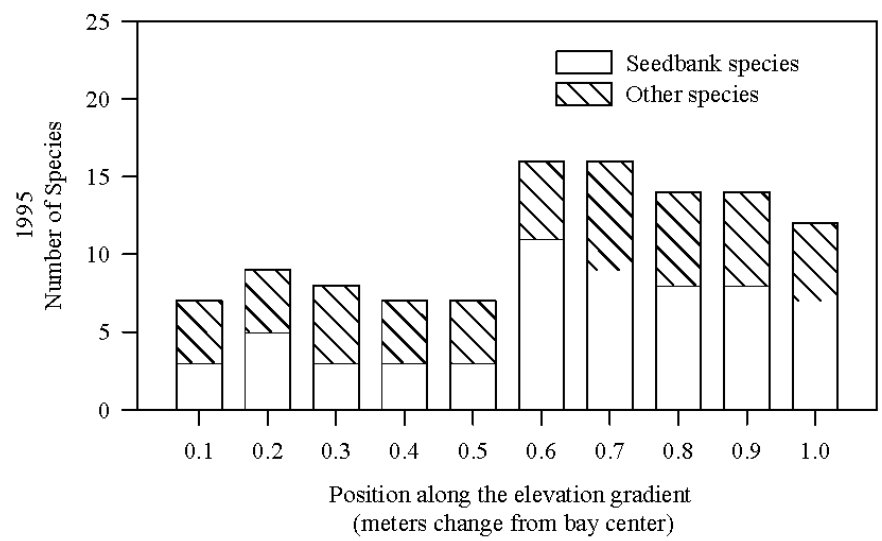
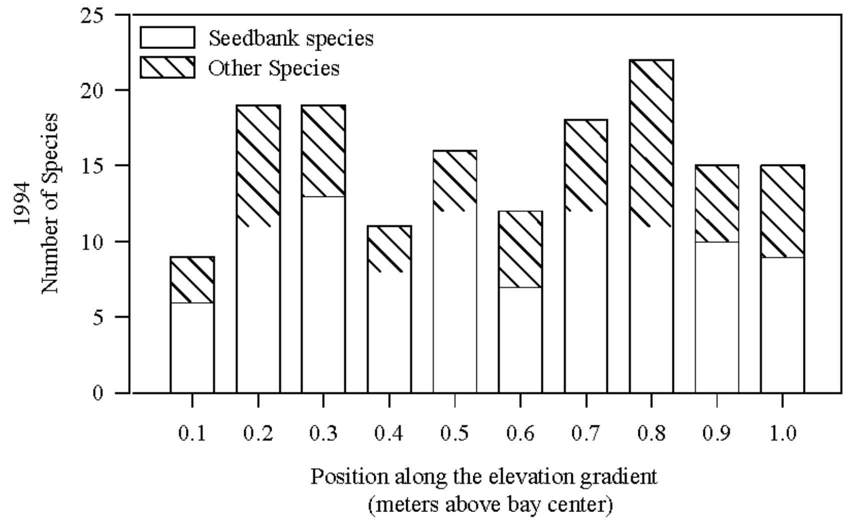


Figure 4. Seed bank recruitment vs. species not found in the seed bank for the Burned / cut treatment area. All vegetation plots along the sample transect were compared to the entire suite of seed bank species.



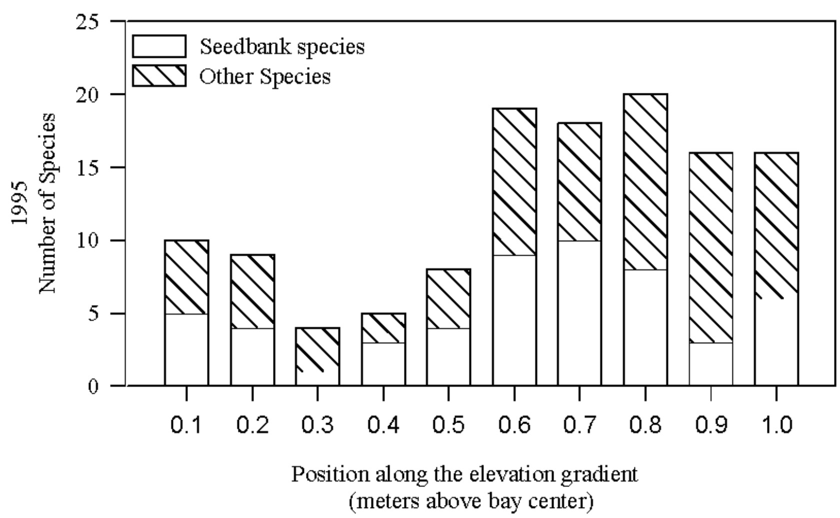


Figure 5. Seed bank recruitment vs. species not found in the seed bank for the Cut treatment area. All vegetation plots along the sample transect were compared to the entire suite of seed bank species.

Table 1. Seed density per m^2 for each position by treatment. Mean density = 146 seeds / m^2 and standard deviation = 103.

	Position					
Treatment	1	2	4	6	8	10
Control	279	176	155	83	83	41
Burned	176	372	103	21	403	31
Burned / cut	155	217	83	155	134	103
Cut	134	279	103	52	21	155

Table 2. Analysis of variance of seed bank species richness and abundance for treatment, position, and interactive effects. Sources of variation are significant at .05.

Seed abundance

Source of variation	DF	Type III SS	Mean Square	F - value	Pr > F
Model	23	50.48	2.19	0.33	0.9947
Error	24	157.50	6.56		
Treatment	3	3.90	1.30	0.20	0.8968
Position	5	12.85	2.57	0.39	0.8495
Treatment*Position	15	33.73	2.25	0.34	0.9823

Species richness

Source of variation	DF	Type III SS	Mean Square	F - value	Pr > F
Model	23	1118.67	48.64	1.12	0.3880
Error	24	1038.00	43.25		
Treatment	3	74.50	24.83	0.57	0.6375
Position	5	376.42	75.28	1.74	0.1637
Treatment*Position	15	667.75	44.52	1.03	0.4612

Table 3. Jaccard similarity coefficients of seed bank and vegetation for treatments by position and year. Kruskal – Wallis χ^2, DF, and exact p – values are given.

1993 ($\chi^2 = 4.18$, DF = 5, p = .3231)

Treatment	1	2	4	6	8	10
Control	0.00	0.00	0.00	0.17	0.00	0.00
Burned	0.00	0.00	0.14	0.00	0.00	0.00
Burned / Cut	0.00	0.00	0.00	0.00	0.00	0.00
Cut	0.00	0.00	0.00	0.00	0.00	0.00

1994 ($\chi^2 = 2.683$, DF = 5, p = .7490)

Treatment	1	2	4	6	8	10
Control	0.00	0.00	0.00	0.00	0.00	0.00
Burned	0.00	0.00	0.33	0.00	0.00	0.00
Burned / Cut	0.17	0.24	0.18	0.16	0.25	0.00
Cut	0.08	0.25	0.17	0.15	0.00	0.33

1995 ($\chi^2 = 5.24$, DF = 5, p = .3870)

Treatment	1	2	4	6	8	10
Control	0.00	0.00	0.00	0.14	0.00	0.00
Burned	0.00	0.00	0.00	0.00	0.00	0.00
Burned / Cut	0.20	0.17	0.00	0.31	0.10	0.23
Cut	0.08	0.15	0.00	0.05	0.00	0.24

Table 4. Jaccard similarity coefficients of seed bank and vegetation for treatments by year. Kruskal – Wallis χ^2, DF, and exact p – values are given.

Treatment	1993	1994	1995
Control	0.04	0.04	0.04
Burned	0.00	0.15	0.05
Burned / cut	0.00	0.44	0.31
Cut	0.00	0.33	0.30

1993 ($\chi^2 = 2.09$, DF = 3, p = .5531)
1994 ($\chi^2 = 5.24$, DF = 3, p = .0090)
1995 ($\chi^2 = 5.24$, DF = 3, p = .0042)

Table 5. Jaccard similarity coefficients of seed bank and vegetation for the entire bay by year.

Year	Similarity
1993	0.06
1994	0.51
1995	0.48

SUMMARY AND CONCLUSIONS

In summary, the restoration treatment chosen for the restoration of Bay 93 showed mixed results. The hydrology of Bay 93 appears to have been restored by simply closing the drainage ditch. Hydrologic data from 1993 to 1994 shows that water levels within the bay were demonstrating patterns typical of other Carolina bay wetlands, with maximum water levels in the late winter and early spring and lowest level in late summer and fall. The hydrologic response took two years to develop, suggesting that an initial period of "priming" may have been necessary for the bay to hold water.

The clear-cut treatment initiated the greatest vegetation response. The initial dry year allowed recruitment across the depth gradient in the bay. Species of different NWI groupings were mixed along the depth gradient in the initial year after restoration treatments. Subsequent flooding removed the upland species from the lower, wetter positions in the bay. Wetland species germinated into the bay and remained for the duration of the study. At the end of 1995, distinct patterns of vegetation zonation were evident in the two clear-cut portions of the bay. Burning had little or no influence on species richness or abundance in Bay 93.

The response of the seed bank, most likely stimulated by the increased light and soil disturbance associated with the clear-cut treatment, was a potential source in providing wetland species to the extant vegetation. As much as 50 percent of the extant species found in Bay 93 also germinated in the seed bank in 1994. More importantly, species typically found in other wetlands were found in the seed bank, and these species germinated into the bay. By 1995, the similarity between the initial seed bank and the extant vegetation had decreased slightly, but wetland species found in the seed bank remained in the clear-cut portions of the bay. The ability of Carolina bay wetlands to respond to simple restoration treatments may be enhanced substantially by utilizing remnant seed banks if they exist.

APPENDIX

Comprehensive species list for Carolina bay 93

* species was present in the seed bank sample
** floating aquatic

Herbaceous:	1993	1994	1995	Annual	Perennial
Acalypha virginica*		X		X	
Andropogon virginicus	X	X	X	X	
Asplenium platyneuron	X				
Carex albolutescens		X		X	
Carex glaucescens*	X	X	X		X
Carex_walteriana		X		X	
Cassia fasciculata		X	X	X	
Croton elliottii		X		X	
Cyperus globulosus		X	X		X
Cyperus haspan*		X	X	X	
Cyperus polystachyos*		X	X	X	
Cyperus psuedovegetus		X	X		X
Cyperus retrorsus*		X	X		X
Cyperus strigosus*		X	X		X
Echinodorus parvulus*		X	X		
Eleocharis elongata		X	X		X
Eleocharis obtusa*		X	X	X	
Erichtites hieracifolium*		X	X	X	
Eupatorium capillifolium*		X	X	X	
Eupatorium compositifolium		X	X		X
Fimbristylus autumnalis*		X	X	X	
Fuirena squarrosa		X	X		X
Galium obtusum	X	X	X		X
Galium filifolium					
Geranium maculatum		X	X		X
Gnaphalium obtusifolium *		X		X	
Houstonia tenufolia		X	X		X
Hypericum gentianoides		X		X	
Iva micracephela *		X	X	X	
Juncus repens*		X	X	X	
Juncus tenuis		X	X		X
Leersia hexandra *		X	X		X
Lespedeeza cuneata		X		X	

Lespedeeza virginica	X	X			X
Linum virginianum		X			X
Ludwigia pilosa		X	X		X
Ludwigia sphaerocarpa		X	X		X
Panicum languinosum *		X	X		X
Panicum scoparium	X			X	
Panicum sphaerocarpon *		X	X		X
Panicum verrucosum		X	X	X	
Phytolacca americana *		X	X		X
Piriqueta caroliniana		X	X		X
Pluchea foetida		X			X
Polypremium procumbens *	X	X	X		X
Psilocarya nitens		X	X	X	
Rhexia mariana *		X	X	X	
Rhexia virginica *		X	X	X	
Rhynchospora chalarocephela		X	X	X	
Rhynchospora pusilla		X	X		X
*Rhynchospora rariflora**		X	X		X
Richardia brasiliensis *		X			X
Rotala ramosior *		X	X	X	
Sabatia quadrangula		X	X	X	
Scleria reticularis			X	X	
Solidago odora *		X	X		X
Utricularia biflora			X	* *	* *
Utricularia inflata			X	* *	* *
Utricularia purpurea		X	X	* *	* *
Viola lanceolata *		X	X		X

Vines*:*

Ampelopsis arboreum	X	X	X
Berchemia scandans	X	X	X
Campsis radicans	X	X	X
Gelsimium sempervirens	X	X	X
Ipomea purpurea			X
Lonicera japonica	X	X	X
Parthenocissus quinquefolia	X	X	X
Rubus spp.	X	X	X
Smilax bono-nox	X	X	X
Smilax glauca	X	X	X
Smilax rotundifolia	X	X	X
Toxicodendron radicans	X	X	X
Vitis rotundifolia	X	X	X

Trees and Shrubs:

Acer rubrum	X	X	X
Callicarpa americana	X	X	X
Cephalanthus occidentalis		X	X
Cornus florida	X	X	X
Diospyros virginiana		X	X
Hypericum hypericoides *	X	X	X
Ilex opaca	X	X	X
Lespedeza bicolor		X	
Juniperus virginiana	X	X	X
Liquidambar styraciflua	X	X	X
*Myrica cerifera**	X	X	X
Nyssa sylvatica	X	X	X
Pinus taeda	X	X	X
Prunus serotina	X	X	X
Quercus nigra	X	X	X
Quercus phellos	X	X	X
Rhus copallina *		X	X
Sassafras albidum	X	X	X
Sorbus americana	X	X	X
Ulmus alata	X	X	X
Vaccinium corymbosum	X	X	X